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A STUDY OF THE PLANKTONIC ROTIFERS OF THE OCQUEOC RIVER SYSTEM, PRESQUE ISLE COUNTY, MICHIGAN¹

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INTRODUCTION

Studies of lotic environments are few compared to those of other aquatic habitats. The number of publications based on stream study and dealing primarily with plankton is probably less than twenty for North America.

The first major work in this country devoted to a study of river plankton was a monumental one—Kofoid (1903, 1908) worked on the Illinois River and published an account of all plankton organisms. Allen (1920) studied a portion of the San Joaquin River around Stockton, California, and likewise included data on phyto- and zooplankton in his report. The entire Ohio River was the subject of investigation by Purdy (1922) who studied the plankton community as well as bottom organisms in an attempt to determine effects of pollution and use of various members of the aquatic habitat as index organisms. Galtsoff (1924) reported on all organisms in the plankton of 465 miles of the upper Mississippi. Eddy (1932) made a study of the Sangamon River, a portion of the Illinois drainage, including the entire plankton assemblage, and later (1934) published an account of fresh-water plankton communities which included several types of aquatic habitats, among them streams. The complete Hocking River basin was investigated by Roach (1932), who studied all plankters of this tributary to the Ohio. Chandler (1937, 1939) reported on the fate of lake plankters when they were drawn into streams by the current at the outlets of lakes; that investigation was carried out at two locations, (1) in a portion of the Huron River in southern Michigan, and (2) in Bessy Creek and Maple River, segments of the larger Cheboygan River drainage in the northern part of the state. Hooper (1947) collected plankton at 23 stations in the upper reaches of the Yukon and Mackenzie systems of Can-

ada and published a report of the qualitative aspects of all the plant and animal elements. The plankton phase of Berner's (1951) limnological study of the lower Missouri River also included both animal and plant constituents. Coopey (1953) determined plankton components in the portion of the Columbia River above and below the Hanford Atomic Products Operation with special observation of any influence of radioactivity on the organisms.

The previous résumé is not an exhaustive list of river-plankton studies but covers the majority of them for this continent. Most of the studies deal with portions of an entire large system and include the total plankton assemblage. Some Europeans have worked in lotic situations but again the number is not great. Carlin (1943) carried on an investigation of an entire stream system in southern Sweden and limited it to the rotifers; he was interested in taxonomy as well as ecological aspects of the Rotifera in the Motalaström. The present study is somewhat similar to that of Carlin's in that it is ecological and deals solely with the rotiferan element in an entire small river system.

I wish to thank F. E. Eggleton for his aid and guidance during the study, A. H. Stockard for the generous use of facilities and equipment of the University of Michigan Biological Station, E. J. Kormondy, R. A. Paterson, W. E. Fennel and many others for their assistance on field trips (Dr. Paterson also identified the aquatic phycomyces), those who so kindly permitted use of their boats on the various lakes, and finally my wife, Harriett E. Beach, who helped in preparation of the manuscript. The work in the summer of 1955 was made possible by a grant-in-aid from the National Science Foundation.

MATERIAL AND METHODS

FIELD

Preliminary investigation of the system was begun in 1952 when qualitative samples were taken

¹ A contribution from the Department of Zoology and the Douglas Lake Biological Station, University of Michigan. Based on a thesis presented in fulfillment of the requirements for the Doctor of Philosophy degree at the University of Michigan.

in some of the lakes during the summer and on a fall trip in November. A similar winter sample was obtained in February, 1953. Intensive study began early in the summer of 1953, continued through 1954, when most of the data were collected, and was drawn to a close at the end of the summer of 1955.

Field study consisted of qualitative and quantitative plankton sampling, physico-chemical determinations, observations on topography and morphometric measurements of the various parts of the system. Much information on the latter phases was gained by examination of U. S. Department of Agriculture aerial photographs of the region.

The majority of the quantitative plankton samples were taken at the surface with a Kemmerer sampler, concentrated by means of a Wisconsin Plankton Net constructed with standard No. 25 silk bolting cloth to a volume of 47 ml measured by a graduated cylinder, and killed, fixed and preserved by 3 ml of commercial formalin previously placed in the storage bottles. The volume of natural water which was strained to produce the concentrated sample varied and was determined in relation to the season and density of the natural population. Experience soon demonstrated that a constant volume was impractical. If only a few Kemmerer-fulls were concentrated when the number of rotifers within the lake was small, as in spring and autumn, the concentrate contained too few animals to provide adequate data. If, on the other hand, many sampler-fulls were concentrated during peak populations, the number of individuals rose beyond the limits needed for an accurate sample of the population. A compromise was therefore struck. In spring and fall, times of low plankton production in this system, 100 sampler-fulls were concentrated. At the beginning of the summer period, when populations were increasing, the number of samplers was reduced to 50, and during mid-summer when populations were at their peak, the number was further reduced to 25 or even 12 in some of the lakes.

Forty-two points throughout the river system were chosen for obtaining data. Field collections were made at least once in each of the lakes except two. A series of samples was taken at selected stations in two of the larger lakes of the system and the river as it entered or left these lakes. Collections in the remainder of the river were made at strategic places along its course with a total of 22 localities visited. Early in the investigation, trips were made to different lakes and parts of the river for samples, but no rigid schedule was kept as to regularity of visits. Once an acquaintance with the situations was made, a more definite program was worked out. In the summer of 1954, from June 16 through August 17, weekly trips were made to the two lakes where the regular stations had been established. Additional trips were made to these lakes on May 8 and 9, September 1, and October 9 and 10 of the same year, resulting in collections in six consecutive months. Additional trips in October of 1953 and March 1955

added to the spring and fall data. An attempt was made to visit all the stations of a given area on the same day and was generally accomplished except for a few times when severe thunderstorms and high winds caused cessation of collecting. Other lakes and parts of the river were visited between the weekly trips in 1954. During the summer of 1955 the river system was covered twice from headwaters to mouth. Throughout the 4-yr period of study a total of 534 preserved samples was accumulated in addition to numerous live samples.

Selected physico-chemical data were also taken. Since the study was mainly biological, complete limnological information was not gathered at all sites. Those items determined were temperature, hydrogen-ion concentration, alkalinity and conductivity. Temperatures were obtained with a Tag pocket thermometer. The pH measurements were made with LaMotte indicator solutions and compared with their standardized color tubes. Alkalinities were measured by standard methyl orange and phenolphthalein titrations (Welch 1948). Conductivity was measured with a Dionic Water Tester. Almost all samples were taken at the surface where previous analyses by other investigators have demonstrated that there is sufficient dissolved oxygen present for the needs of the rotifers. No dissolved oxygen determinations were made, therefore.

LABORATORY

Field collections were examined microscopically in the laboratory. Live samples were kept cool in a portable ice box in the field and refrigerated upon return to the laboratory. This method kept the plankton in good condition on hot summer days and the samples were examined as soon as possible for identification in the live condition. The identifications were made by using the key or description of Ahlstrom (1943) for the genus *Keratella*, of Rouselet (1902) for *Synchaeta*, of Bartos (1948) for *Pedalia*, and of Wesenberg-Lund (1923) for description of male rotifers. Herring's Synopsis (1913) was used for accepted nomenclature, except for recent revisions, and as a source of reference for descriptions of other genera. The publications of Herring & Myers (1922, 1924, 1926, 1928) and Myers (1930), dealing with the rotifer fauna of Wisconsin, were used in identification of several non-eulimnetic forms. Records of species and abundance in live samples made identification easier and more accurate in the preserved material.

A Sedgwick-Rafter counting cell was used for enumeration of the rotifers present. The same cell was used throughout the investigation and a standardized method of subsampling the original samples was followed. In the interest of increasing accuracy, all rotifers in the whole counting chamber were enumerated each time instead of making partial counts and computing the total number in the cell. This eliminated the source of error of sampling the counting chamber which already contained a sample of the

concentrate. Because of the construction of the cell, counts had to be made using the 16 mm objective. In some cases, the morphological details for specific identification could not be observed under this magnification and only generic determinations could be made. No quantitative record of associated organisms was attempted although note was taken of the occurrence of a particularly abundant planktonic genus or lack of associated organisms. Two chamber-fulls were counted for each sample bottle. The record for each station was the result of an average of rotifers contained in two sub-samples from each of the duplicate bottles of concentrated plankton. The results of all quantitative samples were treated mathematically to reduce them to a common expression, that of organisms per liter of natural water.

DESCRIPTION OF THE RIVER SYSTEM

The Ocqueoc River is located in Presque Isle county, the easternmost one of the northern three counties in the lower peninsula of Michigan. It is interesting as a unit because of its completeness within this area. The river drains an area of about 100 sq mi entirely within the western part of the county. The Rainy and Black rivers to the west, and the Trout, Swan and Thunder Bay systems to the east, drain the remainder. The headwaters of the Ocqueoc are located near the southern boundary of the county and the river flows in a general north-northwesterly direction emptying into Lake Huron at Hammond Bay approximately 23 mi north of its source. It winds back and forth through the glaciated landscape and the actual distance traveled by the water is considerably more than 23 mi.

The region is characterized by sandy soils. Most of the uplands are covered with an aspen community, a lesser portion with red, white and jack pine. Some of the land has been cleared for farming but agriculture is not important; the area is hilly, with an esker and drumlins as prominent land forms. The lowlands are generally swampy or marshy and likewise unsuitable for cultivation. For a more detailed description of the system see Beach (1956).

The head-water, or southern, half (Fig. 1) of the system contains nearly all of the lenitic water. Most of this consists of natural lakes resulting from late Pleistocene glaciation. A lesser portion is due to the activities of man. Small dams have been constructed at three places by sportsman's organizations in an effort to improve or enlarge fishing and waterfowl areas. The river flows through five naturally impounded bodies of water: Moore's Lake, Lake Emma, Lake Nettie, Barnhart Lakes, and Ocqueoc Lake. Other lakes apart from the main channel have either permanent or temporary outlets which join them to the river proper.

The river arises in two separate areas, a western and an eastern headwater branch. The western portion begins in *Larix* and *Thuja* lowlands. Such lowlands may be densely wooded areas with a sphagnum



Fig. 1. Ocqueoc River System (southern half). 1. Moore's Lake; 2. Western Swamp Origin; 3. Lake Emma; 4. 1949 Sportsman's Dam; 5. Eastern Swamp Origin; 6. Marl-Bed Lake; 7. 1942 Dam and Floodwater (stippled area is swamp-marsh portion of Upper Floodwater); 8. Unnamed Lake (T33N/R4E/S16); 9. Lake May; 10. Lake Ann; 11. Lake Louise; 12. Lake Nettie; 13. 1939 Dam; 14. Bullhead Lake; 15. Mud Lake (T34N/R4E/S19); 16. Barnhart Lakes; 17. McIntosh Lake; 18. Fox Creek; 19. Little Ocqueoc River. The tributary streams indicated by numbers 18 and 19, and an equal segment of the main river, are duplicated on the map of the northern half of the system (Fig. 2).

groundcover, small pools and trickling streams, or they may be less densely wooded swamps. The latter generally contain shallow water and layers of soft, black, decaying organic matter over a hard sandy bottom but may become completely devoid of water during exceptionally dry seasons, as in the middle and late summer of 1955. Streams flow from the lowland areas and coalesce in the head-water region to form the river. Once formed it continues to flow through bog, swamp and marsh areas of the poorly drained, young, glaciated landscape, and through the naturally or artificially impounded waters, ever increasing in volume as tributary streams

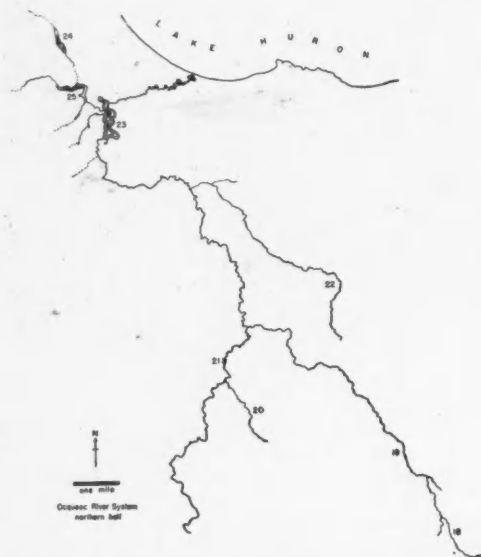


Fig. 2. Oqueoc River System (northern half). 18. Fox Creek; 19. Little Oqueoc River; 20. Indian Creek; 21. Oqueoc Falls; 22. Silver Creek; 23. Oqueoc Lake; 24. Mud Lake (T36N/R2E/S13); 25. Orchard Lake. The tributary streams indicated by number 18 and 19, and an equal segment of the main river, are duplicated on the map of the southern half of the system (Fig. 1).

join it. In all areas there is considerable meandering of the river, even immediately below impoundments. The current is slow and the bottom in most places has a thick layer of organic ooze.

The lower, or northern, half of the system (Fig. 2) contains only three bodies of standing water, Oqueoc Lake, through which the river flows, and Orchard and Mud Lakes which drain into Oqueoc Lake. During its course from the last of the upper lakes, Barnhart, the river flows more rapidly through wooded areas and farm land. There are fewer bogs, swamps or marshes in this part and several streams of ground-water origin join the main river in this segment. It is also in this portion that the river cascades over a Devonian limestone outcrop at Oqueoc Falls. The bottom is covered with limestone rubble immediately below the Falls and varies in the remainder of the course from complete coverage with cobblestones to clean hard sand.

The last segment of the river from Oqueoc Lake to Lake Huron covers a land distance of 2 mi but because of extensive meanders it has a water course of nearly twice that length. The width of the river here varies from about 18 to 30 m and from a few cm to 2m in depth. The shallowest portion is just at the point where the stream flows into Lake Huron over shifting sands caused by waves from the lake and by currents in the river.

POPULATIONS IN THE SYSTEM

WESTERN HEADWATERS

No samples were taken at the inlet to Moore's Lake because the bottom is flocculent, the water very shallow and undoubtedly devoid of plankton. Kofoid (1903) and others have found "age of water," that is, the time it has been contained within a river system, to be very important in plankton production. Since this inlet contained water of recent origin, 1.5 mi before entering the lake, it probably had not had sufficient time to develop a plankton community.

Moore's Lake produced an assemblage which was quite different from most of the other lakes of the system. In the three collections from two years, rotifers and the dinoflagellate *Ceratium* were practically the only zoo-plankters encountered, and few or no green algae were observed. The number of rotifers was high, surpassed only in Oqueoc Lake. The dominant form was *Keratella cochlearis* variety *robusta*, which made up 47-74% of the entire rotifer population. The next most abundant form was generally the typical form of *Keratella cochlearis*. Additional species which occurred regularly in other lakes of the system occurred here also, and accordingly there was no unique fauna as far as quality is concerned.

An outstanding feature of Moore's Lake was the presence of male rotifers in each of the three summer collections (July 22, 1954; June 27 and July 25, 1955). The peculiarity of the situation lies in the fact that although males appeared in the autumn collections from some other lakes, none was found in the summer in those lakes. The species identified was *Keratella cochlearis*, and it occurred regularly. A male was observed hatching from an egg still attached to a female and thus identification was positive. There were few records of males in the preserved material, in spite of records in the live samples, and the males never approached the abundance of females in either live or preserved samples.

The outlet of Moore's Lake would naturally contain some of the lake plankton which was caught in the current. Chandler (1937) demonstrated that such plankton decreases as it flows downstream because of the straining action of plants and removal by the periphyton on the surface of vegetation or other objects in the water. The river from Moore's Lake to Lake Emma is narrow, shallow, contains aquatic vegetation in many places and is certainly conducive to reduction of plankton for these reasons. A sample taken in the river above Lake Emma on June 28, 1955 showed practically no plankton. Only a few empty skins and loricae of limnetic rotifers and a few living individuals of non-limnetic species appeared. These were probably washed off vegetation or swept up from the river bed. Diatoms were the principal algal components and these were rare.

Although the water of the river supports little or no plankton, once it is in the confines of Lake Emma it is again capable of production as evidenced by a rich flora and fauna found there. The plank-

ton assemblage became so thick at times during the summer that the natural water appeared to be like a concentrated plankton sample. The shallowness of the lake (maximum depth about 4 m) is an important factor in production and places nutrients in close proximity to the organisms, especially since the wind can sweep across a flat, open marsh to the northwest and keep the water in circulation. Records indicate that temperatures throughout this lake are, on the average, warmer than in deeper ones which were studied.

There was neither a peculiar rotifer fauna in Lake Emma nor a population outstandingly large for this system. The average number of rotifers for collections taken in June and July of three successive years was about 1,500/liter, with a maximum of 3,600/l occurring July 22, 1954. There was a difference in dominant forms. The genus *Polyarthra*, mostly *P. euryptera*, was generally the most abundant rotifer and made up an average of 36% of the population, with a range of 12-66%. *Keratella cochlearis* and its form *robusta*, combined, were next in abundance, even surpassing *Polyarthra* in a few cases. In 1955 *Pedalia* was as abundant as *Keratella* and in some instances more so. The genus *Synchaeta* was present in all collections but never in greater abundance than the previously mentioned genera in summer samples. In the collections of November 8, 1952 and May 8, 1953, *Keratella*, *Polyarthra* and *Synchaeta* were present, but at these times *Synchaeta* appeared as the dominant form. *Dinobryon* was the main algal component in these two collections. At least 7 other genera of algae were present, as well as representatives of copepods and cladocerans, and these organisms also occurred in summer collections.

The river below Lake Emma for a distance of slightly more than 0.5 mi is similar to a long narrow lake with embayments and backwaters caused by the 1949 Sportsman's Dam. This area might be expected to show little change in plankton from Lake Emma, but a comparison of the total number of rotifers in the outlet bay of Lake Emma with the number present above the dam on July 4, 1955 shows about half as many in the latter situation as in the former. The water is drawn from the lake and travels down the sluggish stream so that by the time it reaches the dam, the abundant vegetation, both floating and submerged, has had an opportunity to strain out part of the plankton. Quantitatively, the rotifer fauna at the dam is essentially the same as in Lake Emma, but not all forms appear reduced in the same proportion and in fact some even show an increase. It may well be that the weedy margins just above the dam serve as favorable habitats for these particular species, and that they thrive in great numbers in the water around the vegetation only to swim too close to the open water, be drawn into the current and swept downstream. A shallow area south of the dam might easily be such a source. A flooded bay in this same region is another possibility, but



Fig. 3. Ocqueoc River below Lake Emma and below 1949 Sportsman's Dam. The narrowness of the channel and the choked up character of the stream is typical of the upper reaches of the system. Note also the narrowness of the grass and sedge filled valley and the characteristic conifer-aspen vegetation of the area.

unlikely since the species present just above the dam are not the abundant ones within the bay.

Immediately above the 1949 Sportsman's Dam the most abundant rotifer was *Keratella cochlearis*, making up 42, 31 and 80%, respectively, of the average population of 420 rotifers/l for three July collections in 1954 and 1955. The two species of *Polyarthra*, *P. euryptera* and *P. trigla*, compose the second most abundant group. Comparing the averages at outlet bay in Lake Emma and at the dam, a 69% decrease was found. The current must be too great for reproduction of those rotifers escaping the straining effects within the river to maintain a population. The dam itself and the river below (Fig. 3) take a greater toll than the part from Lake Emma to the dam, as could be predicted since that lower portion is very narrow, shallow and rich in vegetation. A collection just before the Lake Emma branch merges with the eastern branch yielded 41 rotifers/l and one taken above the 1949 Dam, 7 days before, contained 338/l. The difference is an 88% decrease. A collection in the southern bay of Lake Emma, which consistently showed fewer individuals than the outlet bay, produced 1,612 rotifers. Comparison of this number in the lake with the number in the river above the junction of the two branches gives a decrease of 98%. Although the samples were not made on the same day, it is obvious that there had been a great reduction in plankton in this part of the stream and that the rotifers which Lake Emma contributed had practically disappeared by the time the two upper branches merged.

EASTERN HEADWATERS

No collection was taken at the inlet to Marl-Bed Lake, but since the water is very shallow and of recent origin from seepage, it would probably contain no plankton. As a matter of fact, the lake itself contained very little. Qualitative samples of approximately 70/l on August 16, 1955, produced

about 9 rotifers/l, with *Keratella cochlearis* occurring most frequently, followed by *Synchaeta longipes*, *Synchaeta kitna* and *Polyarthra euryptera*. *Ceratum* and *Dinobryon* were also present in small numbers.

Marl-Bed Lake is probably the least productive of any of the lakes in the system and there is a vast difference between its fauna and that of Moore's Lake, due in all probability to differences both in the basins themselves and in the water they contain. Although both are the first impoundments for their respective sources and each has extensive shallow portions, such areas of Marl-Bed Lake are covered with a limy sediment and are much shallower, therefore subject to maximum temperature variations. Those of Moore's Lake, on the other hand, are covered with decaying organic material and somewhat deeper. Aquatic vegetation is abundant in the latter lake but sparse in the former. Marl-Bed Lake is much closer to extinction than Moore's Lake and such a condition generally shows low productivity.

The outlet from Marl-Bed Lake and another stream of ground water origin flow into, and through the swamp at the upper end of The Floodwater. They are sluggish and deep enough (1 m) to maintain some plankton. Although the water of the easternmost branch may be considered young at the point where it flows under the road 1.5 mi from its source, it still possessed rotifers in a qualitative sample taken May 8, 1953. *Keratella*, *Polyarthra* and *Synchaeta* were present in fair quantities in addition to *Notholca striata*. Several non-limnetic forms *Lepadella*, *Lecane* and *Colurella*, were included, probably having been dislodged from submerged vegetation at the margins. Copepods and cladocerans were present but algal species were more abundant than other plankters. No samples were taken in the east-central stream from Marl-Bed Lake but, because of its similarity to the easternmost one, it probably supported a similar assemblage.

Within the Floodwater there was an excellent opportunity for further development of plankton. The rich vegetation gave shade and decaying matter provided abundant nutrients, hence this shallow area was teeming with life. The open water area, south and west of the swamp portion, had a rotifer fauna well over 5,000/l in early July 1955, but decrease to 1,000/l by the last of the month. This decrease was probably a seasonal fluctuation in part related to the warmer and drier summer of that year. At the earlier date, *Polyarthra euryptera* made up 37% of the rotifer population, followed by *Keratella cochlearis* (21%), *Keratella cochlearis robusta* (18%) and *Gastropus stylifer* (17%). In late July the percentages had shifted greatly in favor of *Keratella cochlearis*, then composing 72% of the population. *Polyarthra euryptera* had been reduced to 10%.

Half-way to the 1942 Dam from the upper Floodwater, the totals had changed to 42% and 19%, respectively, of the population of the upper collecting station for the same 1955 dates. *Keratella cochlearis*

was the most abundant form, composing about half the individuals, *Gastropus* was second in abundance and *Polyarthra euryptera* third. In a 1954 collection of July 22, the total population was about eight times the size of the comparable one of the following year. *Keratella cochlearis* was the dominant form (58%) followed by *Polyarthra trigla* (16%) and *P. euryptera* (13%).

Continuing downstream to just above the 1942 Dam, the samples for the July 1955 dates did not agree in trend. The total population of July 5 had increased slightly while that of July 26 had decreased two and a half times. *Keratella cochlearis* and *Gastropus stylifer* were the two forms occurring most frequently in both samples. Several species increased numerically downstream in the earlier collection: *Keratella cochlearis robusta*, *Polyarthra euryptera*, *Conochilis unicornis* and *Gastropus stylifer*. The last named species also showed an increase in the later July collection. In general, the individual species decreased in numbers downstream with the exceptions previously noted, and some particularly favorable habitat might have been supplying these forms to the current along the way. Otherwise the filtering action of highly vegetated areas is very effective in slowly reducing the entire population.

Even the sluggish current of the river is effective in removing the plankton, but the dam and short section immediately below it accomplishes the removal still more rapidly. From evidence of two collections in two years, the completeness to which the plankton is removed depended partially upon the amount of water present in the stream. In early July 1954, the depth at the collection site 0.25 mi below the dam was approximately 0.5 m, while in 1955, at about the same time and place, it was reduced to about 0.25 m. Debris was common in both collections and the amount of plankton varied considerably between the two years. The total in 1954 was 66 individuals/l while in 1955 the number was 12/l. There is no way of telling in preserved material how many of the individuals of the 66 had been killed or injured by the turbulence of the dam and not yet filtered out by the stream. Undoubtedly some were moribund. Comparing a 1955 collection taken from above the dam a week earlier, the reduction of rotifers was nearly 200 times that taken below the dam. It must be realized that the difference might not be entirely restricted to straining because of the time lapse during which a general plankton decrease could have taken place above the dam, but it is certain that some reduction did occur due to the turbulence of the water and vegetated bed of the river below. Because of the reduction, The Floodwater, although a potentially rich source of plankton, did not contribute a great deal of life to the river.

MIDDLE LAKES REGION

From points below the 1942 and 1949 dams to the place where the two branches merge at The Forks



Fig. 4. Ocqueoc River below The Forks. The western headwater branch enters in the center background. The wider valley and wider meandering channel is typical of the river above the middle lakes region.

and on to Lake Nettie, one might expect an increased development of plankton escaping the turbulence of the dams. The primary reason being that sluggish currents provide more time for the rotifers to reproduce than do swift ones, and certainly this part of the stream is characteristically sluggish. Other inter-related factors are in operation in the stream to keep the number down, however. Shallow water allows rooted aquatic vegetation to develop luxuriously. Such vegetation with its accumulated periphyton filters the plankton out of the moving water, especially at times of low water when the amount of surface area is greater in proportion to water volume. The combination of these factors and which ones are functioning to the greatest degree at any particular time will determine the rotifer, and general plankton abundance.

Small amounts of plankton occurred in the river between The Forks and Lake Nettie (Fig. 4) in spite of the vast vegetated areas within the channel. In two samples from two different years taken about 1.5 mi below The Forks rotifers were present. The relationship between current, water level and vegetation is made evident by comparison of the total number present on different dates: 364/l for July 8, 1954 and 2.1/l for July 12, 1955. The reduction in 1.5 mi in the high water-less vegetation year of 1954 was 45% while in the low water-rich vegetation year of 1955 it was 93%. *Keratella cochlearis* (40%), *Polyarthra euryptera* (19%) and *Gastropus* sp. (14%) formed the majority of the 1954 population. The actual number of individuals found was less at this lower station, indicating that reproduction was not keeping ahead of filtration, but the percentage composition of the dominant forms remained about the same. In addition to the dominant forms, there were present several *Monostyla* and *Lepadella* which are creeping forms, and the alga *Synura* was very common in the 1954 collection. In 1955, debris was fairly common, few *Lepadella* or planktonic forms occurred, and algae were scarce.

About 3.5 mi below The Forks plankton was

still present on July 21, 1953, with 90 rotifers/l occurring, 72% of which were *Keratella cochlearis* and 24% *Polyarthra*. Since this collection was made below Lake Ann, it is possible that the population in the river was partly derived from individuals drawn from the outlet of that lake. A small amount of plankton eventually reached the inlet portion of the river where it emptied into Lake Nettie and this will be discussed later.

Although Lake May is not directly in the course of the river and is connected only by a temporary outlet, a brief discussion is presented here because it is a peripheral part of the system. In three collections, the rotifer population of Lake May was less than in most of the other lakes: 172/l present on August 5, 1954, 357/l on July 14, and 303/l on July 26, 1955. *Kellicottia longispina* composed 52% of the 1954 population and *Conochilis unicornis* 24%. It is unusual for these species to be dominant forms in this system. The same trend was observed in the late July collection of 1955 when *Conochilis unicornis* was the most abundant form (31% of the total). *Kellicottia* was not so abundant, only about 3.5%, but perhaps developed a pulse later. *Keratella cochlearis* was the dominant form only in the early July, 1955 collection (40%) and *Polyarthra euryptera* followed as a second (17%). Otherwise, within Lake May these commonly dominant genera were relegated to a second, third or even lower position of abundance. There was apparently an early pulse of these genera followed by their decline and a *Kellicottia-Conochilis* pulse. Phytoplankton, especially diatoms, was very common in the collections, and may have been the dominant plankton group.

Conditions within Lake May were undoubtedly responsible for the different proportion of organisms. Something had a profound effect on the methyl orange alkalinity (indicating carbonates) because by late July and early August it had dropped from an earlier 11.8 to 7.4 ppm. Since the lake was used as a storage place for logs in the earlier lumbering days and a great deal of bark still remains on the bottom of the lake, the decomposition of this material could easily affect the chemical nature of the water and be reflected in the plankton. Further investigation is necessary to establish exact relationships.

Lake Ann was visited twice in 1955 (July 18, August 1) and showed a well developed plankton assemblage, with 795 rotifers/l on the former date and 826/l on the latter. The dominant species were *Keratella cochlearis* (85 and 81%) and *Polyarthra euryptera* (11 and 15%). *Synchaeta* was not found in either collection. *Ceratium* was fairly common but *Peridinium* was more common in the collections. These two dinoflagellates were characteristic of two other nearby lakes but the rotifer *Limnias ceratophylli*, a form common to the other two areas, was virtually absent in Lake Ann.

Lake Louise, one of these nearby lakes, presented several interesting features. The dinoflagellate *Ceratium* and rotifers made up most of the plankton as-

semblage. The average population of all rotifers during three successive summers was nearly 1,400/l, of which 65% were *Limnias ceratophylli*; *Polyarthra* and *Keratella* alternated in second and third positions of abundance. From the data at hand, *Limnias ceratophylli* appears to reach its peak by mid-July and declines during August. Its very presence in the plankton is unusual. Hudson & Gosse (1886) and Weber (1898) published drawings and descriptions of the animal but always figured it as attached to a substrate, generally plants, and it has usually been regarded as a sessile rotifer. In summer collections from Lake Louise it was always present and always free-swimming, even carrying its tube, and it occurred in too great numbers to be regarded as an adventitious plankton. It is difficult to offer a satisfactory explanation for this repeated occurrence if one continues to regard *L. ceratophylli* as a sessile species. The lake is small and well protected from prevailing winds and as a result there is no significant wave action. The river does not flow through the lake and consequently no major currents are produced. In the absence of wave action and major currents to circulate the water, it appears that *Limnias ceratophylli* is, at least under the circumstances of this lake, a true planktonic rotifer despite the fact it is a tube dweller. Undoubtedly the character of the basin and its water have some bearing on the presence of this rotifer in abundance, the lake being shallow (approximately 3 meters maximum), clear, and possessing a bottom covered with limy sediment. The pH was numerically the highest recorded in the system (8.7) while the methyl orange alkalinity (carbonates) was surprisingly low (8.5-10.7 ppm.).

Collections taken during three years totaled 19 at the inlet to Lake Nettie and of these only 4 exceeded 100 individuals/l. Apparently the straining action of vegetation kept the population down. *Keratella cochlearis* was the most abundant rotifer in all collections except two, one in the spring when *Kellicottia longispina* occurred more frequently and one in early summer when *Polyarthra*, usually the second most abundant form, became dominant. Part of the assemblage there easily could have been derived from Lake Ann since the outlet is not far distant from this collection site. The channel between the outlet of that lake and the station at the inlet of Lake Nettie is deeper, more meandering and generally contains fewer plants than above the outlet. Under such conditions, plankton would have a better chance of survival. Continuing from this station on into Lake Nettie there is a delta area of shallow water and luxuriant vegetation, mainly *Scirpus subterminalis*. The straining action of accumulated periphyton would continue and in all probability little plankton actually gets into the lake in summer. In autumn and spring when the plants have either died down or have not yet reached maximum development, some organisms may be carried into the Lake. An increased number over preceding collections in the fall of 1953 and 1954, and a larger number over several subsequent samples in early summer of 1954

are explained by the fact that plants were observed to be fewer at these times than in mid-summer. Consequently plankton was less effectively removed upstream.

Lake Nettie, together with the river just above and below it, was one of the areas chosen for a more critical study of the rotiferan fauna. It is the largest lake of the system and also near the middle of the entire course. Although the plankton there is qualitatively richest, it is not quantitatively most plentiful. A representative of every species identified through the system was present at one time or another in Lake Nettie but the species did not always reach the abundance found in other lakes. The river at the inlet and the outlet as far down as the 1939 Dam (approximately 1 mi) showed the same qualitative trend with only one or two species of the total number lacking. A variety of algal components was always present in the plankton and *Synura*, *Dinobryon* and *Peridinium* were common to abundant forms in late July and early August. A general decline occurred after that time and algae were actually scarce in the collection of October 9, 1954.

Pedalia was almost always present in the lake with greater populations occurring in July and August. Of the two species present, *P. mira* and *P. insulana*, the former was much more common. On several occasions this genus even surpassed *Synchaeta* in abundance. *Conochilus unicornis* likewise exceeded *Synchaeta* a few times. *Conochilus unicornis* had a mid-June pulse of 70/l and a smaller pulse in mid-August. It was present in all collections except one and showed an increase at 5 m over surface samples taken the same day.

A total of 23 collections was made in the Lake Nettie area, 13 of which were taken from May through October, 1954. The results of these collections are presented graphically. Fig. 5, upper, is a comparison of the plankton entering Lake Nettie by the river, the effects of impoundment on rotifer population, and subsequent effects of the river and a dam on the population from the lake. The number in the inlet was generally less than 100/l during 1954. Two pulses occurred in the river during that year with indications of a third in October. These may reflect pulses in Lake Ann as previously mentioned. The same periods in June, August and October showed pulses in Lake Nettie of much greater magnitude where conditions of impoundment provided a more stable habitat. The outlet, which derives its fauna from the northwestern bay of the lake, likewise showed peak populations for these summer periods. In fact, the August assemblage surpassed the one in the middle portion of the lake. However, there was no October increase at the outlet, but a constant decrease from the August peak to October. The river below Lake Nettie, after traveling about 0.75 mi showed a decided decrease in plankton. The pulses of the lake were reflected here but the straining action of the river had reduced the actual number. The backwater above the 1939 Dam allowed the total population to increase in spring and autumn when

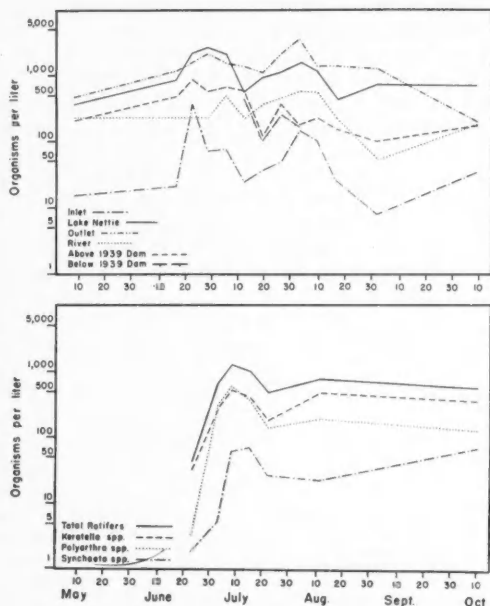


Fig. 5. Upper—Variation in rotifer abundance at stations in the river and its impoundments (Lake Nettie Area) for 1954.

Lower—Seasonal abundance of three common genera and the total rotifer population within Lake Nettie for 1953.

vegetation was not developed to its maximum extent and when water levels were higher. There was less chance at high-water than at low-water stages for the rotifers to come in contact with objects on the bottom, such as stones, and be removed by the periphyton. In summer, when the level was low, however, the above conditions were more effective and the rotifers continued to be removed downstream so that the number of individuals above the dam was less than the number present upstream. In the few samples taken below the dam, after about 25 m of turbulent water, the number showed a further reduction. Undoubtedly many of the individuals collected were moribund due to the effect of turbulence and turbidity and would not have survived long in the river below. These data suggest that a large impoundment, in the form of a lake, is definitely favorable and a smaller impoundment, in the form of a backwater, is generally favorable for development of rotifers, while river conditions are mostly inimical to their production.

Turning to the rotifers within Lake Nettie and the seasonal fluctuations observed there, a similarity will be noted between years. A comparison of the 1954 population (total rotifers in Lake Nettie, Fig. 5, upper) with the total rotifer population of 1953 (Fig. 5, lower) indicates similar trends, and although fewer samples were taken in 1953, an early and a later pulse do show up. These two pulses occurred somewhat later in 1953 than in 1954. If we consider

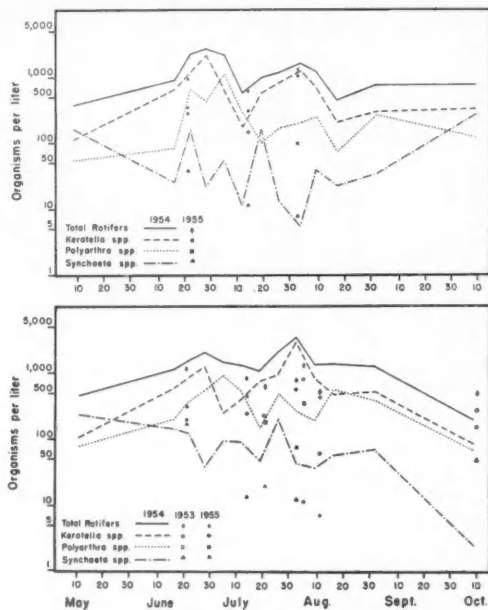


Fig. 6. Upper—Seasonal abundance of three common genera and the total rotifer population within Lake Nettie.

Lower—Seasonal abundance of three common genera and the total rotifer population at the outlet of Lake Nettie.

the symbol for total rotifers in Figure 6, upper, we find that the three collections of 1955 coincide with the trend in 1954.

A consideration of the three most abundant rotifer genera in the center of this lake (Fig. 6, upper) shows *Keratella* and *Polyarthra* to be the dominant forms in most instances. *Synchaeta* seldom approached the abundance of the other two, and was more variable over short periods of time. *Keratella* was usually the most abundant genus of rotifer in the lake and closely followed the fluctuation of the total. In fact, most of the time it was responsible for the pulses. For a short time in June or early July, *Polyarthra* took over as the most abundant rotifer genus, at least at this station.

Subdividing the most abundant genus, *Keratella*, into its constituent species, Figure 7, upper, *Keratella cochlearis* was the principal component with few exceptions. The variety *robusta* was generally next, even surpassing the typical form in a few instances, and the species *K. earlinae* the least numerous of the three, but generally variable in relation to the abundance of the other species. Even though the least abundant of the three within Lake Nettie, this latter species was more plentiful here than anywhere else in the system.

Examination of Figure 6, lower and 7, lower for rotifer populations at the outlet of Lake Nettie shows trends similar to those at the center of the lake. Comparing surface samples at the outlet with those

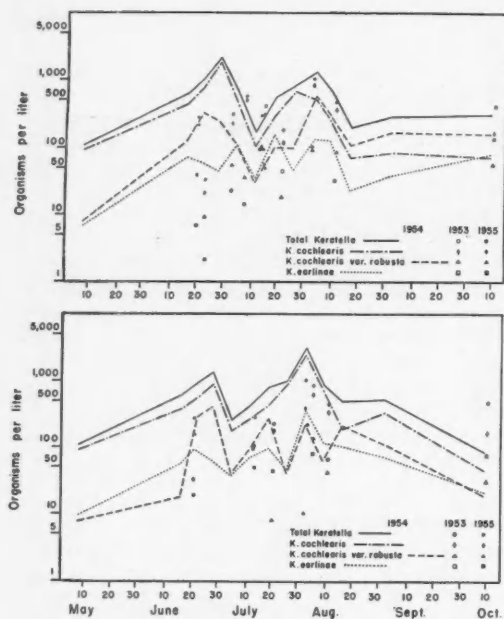


Fig. 7. Upper—Seasonal abundance of species of the genus *Keratella* within Lake Nettie.

Lower—Seasonal abundance of species of the genus *Keratella* at the outlet of Lake Nettie.

at the center of the lake we note: (1) pulses of total rotiferan fauna occurred in late June and early August and were composed mostly of *Keratella cochlearis* (2) the variety *K. cochlearis robusta* and the species *K. earlinae* were variable in abundance and periodicity; (3) *Polyarthra* surpassed *Keratella* again at this station in June or early July; and (4) *Synchaeta* was the least abundant of the three genera during most of the collection period.

Material collected in Lake Nettie and nearby stations in autumn, winter and spring produced proportions of regularly appearing species distinctly different from those characteristic of summer months. On November 8, 1952, *Keratella cochlearis* was the most abundant rotifer which was typical of the system. However, *Synchaeta*, which usually appeared farther down the scale of abundance, was next in frequency of occurrence. This situation was also found on February 28, May 8 and October 10, 1953, on May 8 and October 8, 1954 and on March 12, 1955. In some of these cases *Synchaeta* even appeared to be the dominant rotifer. Evidently the larger sized species, *S. stylata* and *S. oblonga* especially, have a vernal and autumnal pulse in this lake. One fact must be kept in mind, that most of these collections were either near or during the periods of overturn, and species ordinarily present in the lower, cooler regions of the lake could have been brought to the surface. Of course, the overturn was not in effect under the ice during February and March collections, but the presence of these rotifers at colder

water temperatures would again indicate that such temperatures are favorable for this genus. Other forms found during these non-summer collections, and more or less peculiar to such times, were *Kellicottia longispina*, *Filinia longiseta*, *Keratella quadrata*, *Keratella serrulata* and *Brachionus* spp. With the exception of the first two, few individuals of any of these species were present. *Pedalia* occurred in reduced abundance, or was absent, during the periods of colder water. Resting eggs of *Keratella cochlearis* were present in the collection of October 10, 1953 and males were observed in the October 9, 1954 collection.

A collection taken near the middle of Lake Nettie on August 2, 1955, showed a vertical decrease in total population from 1,275 rotifers/l at the surface to 843/l at 5 m. There was a decrease in most species in general, although four major exceptions occurred. *Kellicottia longispina* was not present at the surface but appeared in numbers approaching 30/l at the 5 m depth. *Keratella cochlearis robusta* and *Conochilus unicornis* showed considerable increases with depth as did *Polyarthra trigla* which, however, was not a common rotifer even at 5 m. Perhaps the deeper situation within the lake, because of lower temperatures, is more favorable to the development of these species than are the surface waters.

Observations on the western isolated bay of Lake Nettie re-emphasized the fact that areas within a single lake may differ radically. This portion contained very clear water (as opposed to the highly colored water of the remainder of the lake) and was similar in many respects to Lake Louise and Lake Ann. The first time a collection was made in this bay the concentrated plankton sample was pink in color. Laboratory examination disclosed the color to be due to a large population of *Peridinium*. The dinoflagellates were undergoing division and contained numerous red oil globules. The abundant rotifer was *Keratella cochlearis* composing 80 and 64%, respectively, of the two collections in August, 1954. The next most prevalent group was *Polyarthra* (10 and 21% of the total rotifer population). Specimens of *Limnias ceratophylli* were also present but did not approach the abundance of this animal in Lake Louise. Individuals were more abundant within the bay, however, than in the main part of Lake Nettie where only a few scattered specimens were taken. In 1955 collections, *Limnias ceratophylli* appeared more frequently, averaging 23 per cent of the total for three samples, but with *Keratella cochlearis* remaining the most abundant form, again followed by *Polyarthra*. A sample taken at 5 meters on August 8, 1955, showed an increase in total rotifers from 820/l to 1,240/l. *Keratella cochlearis* showed a slight decrease in actual numbers, and most groups increased only slightly, but *Keratella cochlearis robusta* and *Conochilus unicornis* each showed a considerable increase.

If we now compare the three clear-water areas (Lake Ann, Lake Louise and the western, isolated bay of Lake Nettie), we see the following relation-

ships. Both Lake Louise and the western, isolated bay of Lake Nettie have significant populations of *Limnias ceratophylli*, and in the former this is the dominant species. Total rotifer populations average highest in the isolated bay with *Keratella cochlearis* the most abundant form. Likewise, Lake Ann has a predominance of *K. cochlearis*, although the smallest total rotifer population. *Peridinium* was abundant in the isolated bay but only common in Lake Ann. This latter lake had a considerable population of *Ceratium* and that dinoflagellate was also an abundant plankter in Lake Louise. The clear water of these three lentic areas possibly is not the main factor in faunal differences but does seem to be involved. Chemical composition undoubtedly plays a more prominent role, although physical characters of the basins may be equally important. The shallowness of Lake Louise leads one to this conclusion, since it is a factor not present in the other two deeper lakes. Higher pH, accompanied by higher phenolphthalein alkalinity (bicarbonates) but lower methyl orange alkalinity (carbonates), of Lake Louise may be some of the chemical factors responsible for its faunal differences. It is certainly possible that other chemicals are in part accountable for the variations of these bodies of water from others in the system and additional work is necessary for any definite conclusions.

Bullhead Lake (Fig. 8), from which three samples were taken, has little in the way of a special rotifer fauna to distinguish it from the other lakes, although it has quite a different basin. The typical form of *Keratella cochlearis* was abundant in two collections and the variety *robusta* exceeded it in one. *Polyarthra euryptera* ranked second in abundance. *Pedalia* was well represented in the single 1954 collection with 79 individuals/l, but was absent or rare in 1955. In a single collection, taken July 18, 1955, *Gastropus hyptopus* was present in quantities amounting to 37/l, or almost 19% of the total population, but it was not present in any other sample. The genus *Synchaeta* was entirely absent from all 1955 collections. Although this lake has pH values close to those of Lake Louise, with methyl orange and phenolphthalein alkalinities very similar, there were no *Limnias ceratophylli* found in any samples therefrom. One very obvious difference between these lakes is that the water of Lake Louise is clear; that in Bullhead Lake highly colored. This fact and the reasons for coloration or lack of it might in part explain the lack of *Limnias* in the latter situation. In spite of a population totaling at least 330/l in this lake, it is unlikely that any rotifers from it get into the river. The outlet frequently dries up during the summer and the length (0.75 mi) combined with the narrowness of the channel would very quickly remove any floating organisms.

From previous discussion, it will be recalled that river conditions below Lake Nettie are generally unfavorable for plankton increases and the quantity is actually reduced by the time the 1939 Dam is reached. The actual loss at the dam is not great, generally less



Fig. 8. Bullhead Lake. This lake, although small, is typical of the majority of lakes in the system—shallow margins with considerable vegetation and bounded on at least one side by high hills (part of an esker) covered with conifers and aspen.

than 20%. However, a sample taken 0.25 mi below the dam had a very sparse population of rotifers. Removal may have been due to either of two things: the effect of turbulence at the dam, which kills or injures the animals, or the straining action of the river, since it is very shallow and often covered with cobblestones in this area. It is very likely a combination of the two factors which reduces the number. The river deepened somewhat below the collection site 0.25 mi below the dam, and became more sluggish, thereby decreasing the filtration effect, because some plankton survived to flow into Upper Barnhart Lake. Filtration had about the same effect on all species and accordingly *Keratella cochlearis*, *Polyarthra euryptera* and *Polyarthra trigla* were the most abundant forms entering the lake.

Within the Barnhart Lakes, the rotifer populations did not differ in quality, but the Lower Lake had a greater total population. Differences in the basins themselves and the location of the lakes with respect to the river and each other may be partly responsible. The Upper Lake is deeper (22 m) with fewer areas for vegetation and is constantly diluted with inflowing water, while the Lower Lake is not so deep (6 m), contains more plants, and receives water from the shallow bay of the upper one. Over half of the individuals in both portions were *Keratella*, with *K. cochlearis* forming an average of 70% of that genus. *Polyarthra* was next in abundance, about one-fifth to one-eighth of the total, and was composed of an average of 76% *P. euryptera*. *Synchaeta* was not well represented and other genera frequently exceeded it in abundance. In spite of the large total population of rotifers in the Lower Lake, few were transported far in the river because of the character of the outlet. It was only 15-30 cm deep, with a carpet of *Chara* covering the bottom and frequently coming to the surface. A comparison of the total population of 541 rotifers/l in the lake with 73/l taken about 0.5 mi below the actual outlet on the same day serves to illustrate the effect.

McIntosh Lake is another lentic area which is

connected to the river by a temporary outlet. Because this outlet is so narrow and shallow, it probably carries no plankton into the river. The lake itself had a population which was always in excess of 500 individuals/l and frequently greater than 1,000/l. Algae were generally abundant with *Synura* and *Dinobryon* common forms. *Keratella cochlearis robusta* was abundant and composed the dominant group in two out of four collections; the typical form was also abundant in some of the collections. *Polyarthra* was likewise well represented. In averages of four samples taken during three years, *K. cochlearis robusta* amounted to 27%, *K. cochlearis* 20%, and *Polyarthra* 21%. Other species which were frequently common in the collections included *Keratella earlinae*, *Synchaeta stylata*, *Gastropus stylifer* and *Chromogaster ovalis*. The abundance of plankton in this small lake is no doubt due, in part, to a nearby farm yard and field which supply nutrients by runoff.

CENTRAL RIVER PORTION

Barnhart Lakes are the last lentic areas through which the river flows before it enters Okechoc Lake, about 19 mi downstream. None of this entire span is conducive to plankton development. The current is generally swift and often the water flows over shallow rubble covered bottoms. Even if large quantities of plankton were poured into the river by the last lake, conditions are not favorable for its development. Furthermore the outlet bay of Lower Barnhart Lake is very effective in removing almost all the plankton.

Three tributaries, Indian Creek, the Little Okechoc River and Silver Creek, enter the main stream before it reaches Okechoc Lake and act as dilutents of the water in the main channel. There are no impoundments occurring along these streams to provide favorable habitats for plankton development and the tributaries may be considered to contain young water which has not had sufficient time to develop a limnetic rotifer assemblage.

A sample taken in the river at the M-69 highway bridge about 0.5 mi above Okechoc Falls showed abundant quantities of debris, scattered algal cells, which were probably moribund, and one *Lepadella*, a non-limnetic rotifer. Any plankton which Lower Barnhart Lake might have contributed to the river had been filtered out or destroyed in the 9 mi between these two points. Another sample was taken less than 0.25 mi below Okechoc Falls to determine whether any possible sessile organisms, including rotifers, might have been washed off the rocks in that turbulent portion of the stream. Any living rotifers in such a sample would obviously have come from the area of the Falls and survived the turbulence, since virtually no living organisms had been found in the water immediately above. Only a few living algal fragments, washed from the rubble, were found, and no other identifiable organisms were observed. This plankton-sterile condition continued all the way to Okechoc Lake since qualitative and quan-

titative samples taken in the river above that lake produced only large quantities of debris, a few algal cells, mostly diatoms, and scattered non-limnetic rotifers of the genus *Lepadella*, which had been picked up by the river in the 10 mi between the Falls and the inlet. The condition of these latter organisms, whether living or dead, could not be ascertained in these samples, all of which were preserved prior to examination.

LOWER LAKE REGION

Once again the impounding action of Okechoc Lake allowed rotifers to develop. Quantitatively, the lake produced the largest amounts of both phyto- and zooplankton in the whole system although the actual number of species present was not the greatest. The fact that this last lake in the system has the richest fauna, numerically speaking, is not surprising, since limnologists have reported the phenomenon before. The age of the water is greatest and such a lake receives the benefit of all the nutrients gathered by the river along its course. The sinuosity of the shore line, the rich vegetation, fertilization from a pasture at the southern end, and perhaps a small amount of pollution from a resort on the east side of the lake are all factors which tend to increase production. By mid-summer the water appeared to be almost pea soup with *Synura* and *Dinobryon* the organisms responsible for the color. The part of the lake south of the island was more productive as measured by the abundance of algae and reflected in the rotifer populations (Figure 9). Study of the graph for the southern part of the lake (Fig. 9, upper) shows that *Keratella* made up most of the total number of rotifers at all times when collections were taken. The species *K. cochlearis* composed the greatest percentage of the genus and there were occasions when the zooplankton element of the lake was practically a pure culture of that species. *Keratella cochlearis robusta*, on the other hand, was poorly represented, except for July and August, 1955, and *K. earlinae* was very scarce in the entire lake throughout the investigation. *Polyarthra* usually occupied second position of abundance in the southern part of the lake, but *Synchaeta* surpassed it on two occasions, and these *Synchaeta* pulses occurred earlier than the early summer *Keratella*-*Polyarthra* and total rotifer pulses.

The population in the Group Camp, or northern, Bay was more variable in character (Fig. 9, lower) but did show pulses less in amplitude and slightly in advance of those at the inlet end of the lake. In the early part of the season, *Keratella* was the dominant form with *K. cochlearis* again forming almost a pure culture. *Polyarthra* was extremely variable in this part of the lake and was even the dominant form in one collection. Generally, it was the least abundant genus of the ones represented on the graphs. *Synchaeta* was likewise somewhat variable in abundance but that was partly due to a variation of species during the course of the summer. There are two groups of *Synchaeta* present in the lake, a group

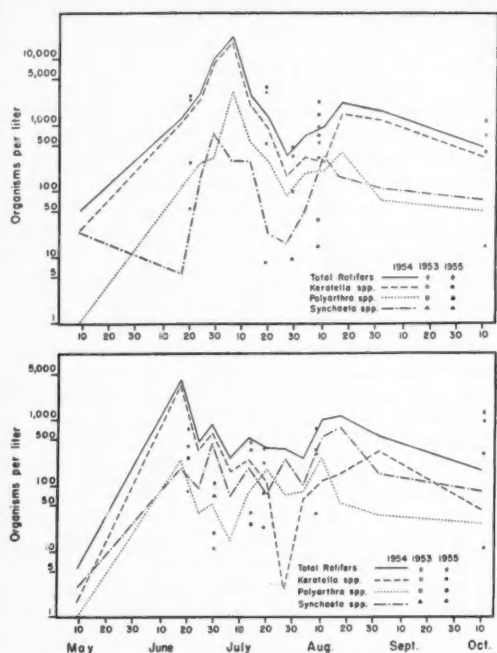


Fig. 9. Upper—Seasonal abundance of three common genera and the total rotifer population in the southern half of Ocqueoc Lake.

Lower—Seasonal abundance of three common genera and the total rotifer population in the Group Camp (northern) Bay of Ocqueoc Lake.

composed of large sized individuals and including *S. stylata*, *S. longipes* and *S. pectinata*, and the single small sized species, *S. kitna*. The early pulses in June and July were generally due to the predominance of the former group, while the August pulse was due to the latter, and for a short time that species again formed practically a pure culture in the lake as far as zooplankton is concerned. The trend of large sized species, dominant in late summer, also occurred in the southern portion of the lake. The only other well represented group in this lake was *Gastropus* which was present in nearly all the collections.

Subsurface samples at 2.5 and 5 m were taken in this lake to determine what differences occurred in vertical distribution. In general, there was a decrease with depth for all species except *Conochilis unicornis* which increased in almost every case. Campbell (1941), working in the depressions of Douglas Lake generally exceeding 20 m, found highest populations of this species near the 5 m level. Total populations of rotifers in Douglas Lake tended to decrease to depths around 10 m and then, on occasion, to increase below 15 m. Ocqueoc Lake does not reach such depths. On the other hand, the gradual decrease of all species, except *Conochilis unicornis*, with increased depth which Campbell demonstrated in Douglas Lake, was apparent in Ocqueoc

Lake. Neither sufficient samples nor enough physico-chemical data were accumulated in the present study to justify further discussion of the similarity between the two lakes.

In autumn and spring collections, *Keratella cochlearis* was the principal rotifer, making up 45% or more of the total. Males of *K. cochlearis* were present in the samples taken in October 1953 and 1954, and resting eggs occurred, but rarely, in the 1953 collection. Other species, occurring sparingly in these off-season collections and not ordinarily found in the summer, were *Notholca striata*, *Kellicottia longispina*, *Keratella quadrata*, and *Brachionus* spp. The protozoan *Codonella* was a common associated plankton on October 10, 1954. In a sample taken from under the ice, March 12, 1955, the dominant forms were *Notholca striata* and *Brachionus* spp., although they were not common. A few strands of the diatom *Fragellaria* were present but regularly appearing rotifer species of *Keratella*, *Polyarthra* and *Synchaeta* were almost never encountered in this winter sample.

Mud Lake (T36N/R2E/S13), which drains into Orchard Lake in times of high water, was visited for one qualitative and one quantitative sample. The qualitative one was taken from the edge while standing in the water and the quantitative one from a boat in the center of the lake; the results of the two samples were quite different. The latter is probably a better representation of the limnetic fauna and showed a total population on July 29, 1954, of 520 rotifers/l, of which 85% were *Keratella cochlearis*. *Synchaeta* was completely absent from the sample and indeed few other genera, or even individual rotifers, were present. The dinoflagellate *Ceratium* was abundant in this collection. The qualitative sample of June 30, 1953 showed *Polyarthra trigla* as the dominant form with few *Keratella* or other genera present. The general characteristics of this basin, being only about one meter deep and with a soft, flocculent bottom, undoubtedly have a profound affect upon the fauna produced here. Because of the temporary nature of the outlet and its shallowness when it is draining the lake, probably no plankton ever reaches Orchard Lake from Mud Lake.

Orchard Lake, with a long, narrow outline and a declivity well covered with vegetation, has a rotifer fauna averaging over 1,250 individuals/l in three collections taken in the latter part of July and early August, 1954 and 1955. On July 29, 1954 *Polyarthra euryptera* composed 67% of the population and *Keratella cochlearis* formed about 17%. The opposite condition occurred in 1955 when either the variety *robusta* or the typical form of *K. cochlearis* composed over half of the population. In the July collections of 1954 and 1955, *Glenodinium* was the abundant associated form while by August, 1955, *Peridinium* had taken over and *Synura* was common. The rotifer genus *Synchaeta* was not encountered in any of the 1955 samples and was not well represented in the 1954 collection. Although a high rotifer population exists in the lake, it is unlikely that any of

it gets into Oqueoc Lake because the outlet is very shallow, sinuous and, in times of high water, carries large amounts of silt by the time it reaches Oqueoc Lake. All these factors tend to remove any plankton which might leave Orchard Lake.

Three stations were set up below Oqueoc Lake, one immediately below the lake, another about 80 m downstream, and a third 80 m beyond the second. Originally it was thought that a relationship between plankton removal and distance traveled by the stream could be demonstrated. Station II was discontinued when it was found that in the 1953 collections there was an apparent increase between it and Station I. Comparing the records of Stations I and III there were variations extending from 69% reduction to an actual increase in total planktonic rotifers in this section of the stream. Other factors than mere distance must be involved. In general, however, the results show that the river carried less plankton per liter (even at Station I) than was present within the Group Camp Bay and that plankton did decrease while passing 160 m downstream. There were exceptions at times.

During the 3.75 mi from the last station below Oqueoc Lake to the mouth of the river, most of the plankton was removed. Of the large number of rotifers present at Station I below Oqueoc Lake, a maximum of only 3% ever reached the station about 160 m above the actual mouth of the river, and these individuals could conceivably have been removed before the water flowed into Lake Huron. Phytoplankton was somewhat more successful in survival, especially *Synura* and *Dinobryon* which were so abundant in Oqueoc Lake. Occasional specimens of *Ceratium* and *Codonella* appeared but had probably been swept up from the bottom. On the whole, however, very few rotifers, or for that matter any plankters are ever contributed to Lake Huron by the Oqueoc River system in spite of the fact that large quantities are produced at various points along its course, even within a distance of less than 4 mi above the mouth of the river.

DISCUSSION

The genus *Keratella* was present in all collections and if any one rotifer were chosen as typical of the system, *Keratella cochlearis* would be the choice by necessity. This is a ubiquitous, perennial species and is mentioned in almost all studies of plankton. Allen (1920) found it to be the most numerous species in two out of his three stations in the San Joaquin River and likewise it was one of the more important constituents of the rotifer fauna in Carlin's work (1943) on the Motalaström. It does not always rank first in abundance, as found by Kofoid (1908) in the Illinois River, but generally is well represented. In this study, *Keratella cochlearis* definitely showed a greater abundance in summer and, in the two lakes studied more intensively, appeared to be diyclic with pulses in early and late summer. The early one was generally larger. Eggs were present in collections taken in all seasons. A fre-

quent observation of this species was that those individuals collected within the channel of the river usually had a shorter posterior spine than those in lakes. There is much in the literature on the problem of cyclomorphosis but, to my knowledge, no actual experimental work with this species has been done. Temperature is believed to be the controlling factor. The river and lakes in this system often had practically the same temperature on the same days but the short spined forms appeared more prevalent in the lotic habitat. Precise records of either spine length or number of individuals were not kept, hence no positive statement can be made, but it appears that current, perhaps along with temperature, had an influence on the length of the posterior spine.

As has been previously mentioned, males of *Keratella cochlearis* occurred in autumn samples of Lake Nettie and Oqueoc Lake. They were also taken in all three summer collections from Moore's Lake, in two different years, but this must be regarded as unusual. Parthenogenesis is the general method of rotifer reproduction with males occurring infrequently, generally during only a few weeks of unfavorable ecological conditions, such as those preceding drying up of a pond or approach of winter. At these times, males are produced by a special generation of females, mictic, which undergo a meiotic division. In parthenogenesis the amictic female produces eggs which undergo one non-reductional division. Different workers in the field have assigned various chemical, physical or biological conditions to the production of mictic females but the precise factors which produce them are not definitely known, if indeed any single factor is responsible. Such things as the quality and quantity of food, temperature, and chemical composition of the water have all been designated as the determining factor after experimental studies using various genera. In natural waters it seems more than likely it is not any single factor, but rather a complex relationship of several which are responsible for production of mictic females followed by males. Different factors or thresholds of these conditions may be necessary in different genera or species.

Within Moore's Lake the temperature at the time of collections was well above the fall temperatures in the other lakes producing males, and was not as high as that encountered elsewhere during the summer. Therefore, extremes in temperatures per se hardly seem responsible for the appearance of males in this lake. Of the waters tested, the chemical composition of this one was very similar to those from other parts of the system (Table I), so this factor as such may be ruled out at least until more elaborate analyses have been made. It appears that food relationships have a more definite bearing on the problem. There is no agreement among workers about the exact relationship between food and mictic female production, but Wesenberg-Lund (1930) summarizes the several experimental works on the problem by the statement, "It is the change of food in both directions from *Chlamydomonas* to *Polytoma* and from

Polytoma to *Chlamydomonas*, . . . which cause the appearance of mictic females." He emphasizes the change as the important thing.

If we consider the mechanism of feeding in rotifers and the material available within Moore's Lake which could serve as their food, we find different genera feed on different substances. *Keratella*, *Conochilis* and *Collotheca* are among those genera which Pennak (1953) lists as having a mastax of the type capable of utilizing detritus and phytoplankton. All the other planktonic rotifers occurring in this lake have a type specialized for predation. *Chromogaster* is one genus that is known to utilize dinoflagellates (Kolisko 1938) and many times in my collections *Asplanchna* has been observed to contain individuals of the genus *Keratella* in its digestive tract. With a constantly large population of *Keratella* or dinoflagellates, which occur in the lake, predaceous genera are capable of maintaining themselves. The question is, then, how is the large population of *Keratella* actually supported in Moore's Lake? The character of the lake itself may provide the answer. The bottom of the extensive shoal area is covered with a layer of flocculent organic detritus which is one possible source of food. Currents within the lake probably keep minute particles of this material in circulation. Bacteria undoubtedly utilize this organic material and are in turn fed upon by rotifers. If there is an early algal bloom (undetermined in this study) which disappears by June, this change in food substances, from living green cells to dead organic matter or bacteria, could be responsible for mictic female, and eventually male production.

Another influence tending to produce males may be exerted by crowding. Ahlstrom (1933) found that the number of rotifers captured in plankton samples varied from 20 to 4,619/l in pond conditions. Pennak (1953) states that the average number of planktonic rotifers in lakes varies from 40 to 500/l, "with populations in excess of 1,000 per liter being unusual." This latter number was exceeded by at least 2,000 in Moore's Lake. The effect of crowding might be to impoverish the food supply and cause starvation, or perhaps to change the chemical composition of the water by the accumulation of metabolic products. Shull (1910, 1911), working experimentally, concluded that both could have an effect. Since *Keratella cochlearis* was the most abundant species and all the males present were members of this species, there appears to have been a correlation between crowding and production of males. It is recognized that the factors in the production of males are complex and that others in addition to those reported may have been operative at the time when Moore's Lake was being studied.

The variety *Keratella cochlearis robusta* was well represented in collections from this system and in a few instances even surpassed the typical form. Ahlstrom (1943) stated that the variety was not common in material which he studied. This was not the case in the area under investigation here. Few au-

TABLE 1. Physico-chemical data of selected stations of the Ocqueoc River system, Presque Isle County, Michigan.

| Locality | Date | Water temp. °C. | pH | ALK. ¹ PPM. | | Cond. ² |
|----------------------------|---------|--------------------|-----|------------------------|------|--------------------|
| | | | | ph-th | M.O. | |
| Moore's Lake..... | 7-7-53 | 24 | 7.8 | 0.4 | 13.2 | 225 |
| | 7-22-53 | 24 | 8.1 | 0.35 | 12.7 | 250 |
| | 6-27-55 | 19 | 8.0 | 0.37 | 14.1 | |
| | 7-25-55 | 23 | 8.2 | 0.8 | 13.9 | |
| Inlet, Moore's Lake..... | 7-25-55 | 18 | 7.4 | — | 17.7 | |
| Ocqueoc River below | | | | | | |
| Moore's Lake (at Road) | 7-7-53 | 22 | 7.6 | — | 14.0 | 240 |
| | 7-1-54 | 22 | 7.4 | — | 12.3 | 210 |
| | 6-28-55 | 21 | 7.7 | — | 14.0 | |
| Stream of Western Swamp | | | | | | |
| Source..... | 7-7-53 | 16 | 7.1 | — | 14.0 | 240 |
| | 7-1-54 | 16.5 | 7.2 | — | 13.3 | 225 |
| | 6-28-55 | 15 | 7.2 | — | 15.5 | |
| Bay off Ocq. R., upper end | | | | | | |
| of marsh above L. | | | | | | |
| Emma..... | 6-28-55 | 17 | 7.4 | — | 14.1 | |
| Inlet to Lake Emma..... | 6-28-55 | 21 | 8.0 | 0.8 | 13.8 | |
| Southern Bay of Lake | | | | | | |
| Emma..... | | | | | | |
| | 6-21-54 | 24 | 8.0 | — | 12.0 | 210 |
| | 6-27-55 | 21 | 8.3 | 0.8 | 12.3 | |
| | 7-25-55 | 25.5 | 8.4 | 1.3 | 12.1 | |
| Outlet Bay of Lake Emma | | | | | | |
| | 7-7-53 | 23.5 | 8.2 | 0.7 | 12.0 | 210 |
| | 7-4-55 | 27 | 8.4 | 0.6 | 12.8 | |
| Bay south of 1949 Sports- | | | | | | |
| man's Dam..... | | | | | | |
| | 7-4-55 | 29 | 8.2 | 0.8 | 12.8 | |
| | 7-25-55 | 28 | 8.2 | 0.6 | 12.7 | |
| 1949 Sportsman's Dam.... | | | | | | |
| | 7-1-54 | 26 | 7.8 | — | 12.5 | 225 |
| | 7-22-54 | 27 | 8.0 | 0.6 | 12.7 | 240 |
| | 7-4-55 | 28 | 8.0 | 0.3 | 13.1 | |
| | 7-25-55 | 25.5 | 8.0 | 0.5 | 12.5 | |
| Below 1949 Dam at The | | | | | | |
| Forks..... | | | | | | |
| | 7-8-54 | 23 | 7.8 | — | 12.3 | 210 |
| Ocqueoc R., Eastern | | | | | | |
| Swamp-marsh Source at | | | | | | |
| Road..... | | | | | | |
| | 7-1-54 | 21 | 7.1 | — | 10.9 | 165 |
| | 7-26-55 | 28 | 7.4 | — | 15.5 | |
| Marl-bed Lake..... | 8-1-55 | 22 | 7.9 | Trace | 16.6 | |
| Outlet of Marl-bed Lake | | | | | | |
| at Road..... | | | | | | |
| | 7-26-55 | 28 | 7.6 | — | 14.6 | |
| Upper Floodwater..... | | | | | | |
| | 7-5-55 | 29 | 8.0 | 0.5 | 13.9 | |
| | 7-26-55 | 26 | 8.0 | 0.6 | 14.9 | |
| Ocq. R. midway to 1942 | | | | | | |
| Dam from Floodwater.. | | | | | | |
| | 7-5-55 | 29.5 | 8.0 | 0.2 | 13.9 | |
| | 7-26-55 | 25 | 8.0 | 0.6 | 14.0 | |
| 1942 Dam..... | | | | | | |
| | 7-5-54 | 29 | 8.0 | 0.3 | 12.8 | |
| | 7-26-55 | 26 | 8.1 | 0.7 | 12.7 | |
| Ocqueoc River, below 1942 | | | | | | |
| Dam..... | | | | | | |
| | 7-8-54 | 21 | 7.8 | — | 11.5 | 190 |
| | 7-12-55 | 27 | 8.0 | 0.3 | 13.2 | |
| 1.5 miles below The Forks. | 7-12-55 | 25 | 7.6 | — | 14.4 | |
| Lake May..... | | | | | | |
| | 8-5-54 | 23 | 8.0 | — | 7.0 | 130 |
| | 7-14-55 | 26 | 8.2 | 0.42 | 11.8 | |
| | 7-26-55 | 26 | 8.2 | 0.35 | 7.4 | |
| Lake Ann..... | | | | | | |
| | 7-18-55 | 25 | 8.4 | 0.8 | 12.0 | |
| | 8-1-55 | 27 | 8.4 | — | — | |
| Lake Louise..... | | | | | | |
| | 7-8-53 | 22 | 8.5 | 0.9 | 10.7 | 160 |
| | 8-5-54 | 23 | 8.4 | 0.8 | 9.5 | 180 |
| | 7-14-55 | 27 | 8.7 | 1.2 | 8.5 | |
| | 8-1-55 | 28 | 8.7 | — | — | |

TABLE 1. (Continued)

| Locality | Date | Water temp. °C. | pH | ALK. ¹ PPM. | | Cond. ² |
|---|----------|--------------------|-----|------------------------|------|--------------------|
| | | | | ph-th | M.O. | |
| Ocequeoc River, Inlet to Lake Nettie..... | 5-9-54 | 9 | 7.6 | — | 10.4 | 165 |
| | 6-22-54 | 20.5 | 7.6 | — | 11.8 | 190 |
| | 10-9-54 | 11.5 | 7.4 | — | 12.0 | 210 |
| | 6-21-55 | 24 | 7.8 | | | |
| | 7-12-55 | 23 | 7.8 | 0.35 | 15.1 | |
| | 8-2-55 | 27 | 8.0 | | | |
| Middle Portion of Lake Nettie..... | 2-28-53 | 0.5 | 7.3 | — | 13.8 | 240 |
| | 7-3-53 | 22.5 | 8.0 | 0.3 | 12.1 | 210 |
| | 10-10-53 | 13 | 7.8 | | | |
| | 5-8-54 | 10 | 7.8 | — | 11.7 | 200 |
| | 6-22-54 | 23 | 8.0 | — | 11.6 | 195 |
| | 10-9-54 | 13 | 7.8 | — | 12.6 | 225 |
| | 3-2-55 | 1 | 7.2 | — | 11.5 | 190 |
| | 6-21-55 | 24 | 8.3 | | | |
| | 7-14-55 | 26 | 8.3 | 0.5 | 12.5 | |
| | 8-2-55 | 27.5 | 8.4 | 0.6 | 12.9 | |
| Western Isolated Bay of Lake Nettie..... | 6-21-55 | 25 | 8.2 | | | |
| | 7-14-55 | 28 | 8.4 | 0.7 | 13.4 | |
| | 8-2-55 | 27 | 8.3 | 0.7 | 13.2 | |
| | | | | | | |
| Ocequeoc River, Outlet of Lake Nettie..... | 5-8-54 | 10 | 8.0 | — | 12.3 | 200 |
| | 6-22-54 | 22.5 | 8.2 | — | 12.0 | 200 |
| | 10-9-54 | 12 | 7.9 | — | 12.8 | 225 |
| | 6-21-55 | 25 | 8.4 | | | |
| | 7-14-55 | 27 | 8.4 | 0.6 | 11.8 | |
| Ocequeoc River, between Lake Nettie and 1939 Dam..... | 5-8-54 | 9 | 7.8 | — | 11.8 | 200 |
| | 10-9-54 | 12 | 7.8 | — | 12.6 | 225 |
| | 7-3-53 | 22 | 7.7 | — | 12.7 | 210 |
| | 10-10-53 | 14 | 7.8 | | | |
| | 5-8-54 | 8 | 7.7 | — | 12.2 | 200 |
| | 6-22-54 | 23 | 7.8 | — | 12.1 | 200 |
| 1939 Dam..... | 10-9-54 | 12 | 7.6 | — | 12.9 | 225 |
| | 6-21-55 | 24 | 7.7 | | | |
| | 7-14-55 | 28.5 | 8.2 | 0.4 | 12.0 | |
| | 8-2-55 | 27 | 7.8 | | | |
| | | | | | | |
| | | | | | | |
| Bullhead Lake..... | 8-5-54 | 23 | 8.3 | 0.3 | 10.2 | 190 |
| | 7-18-55 | 28.5 | 8.6 | 1.0 | 10.5 | |
| | 8-1-55 | 29 | 8.6 | | | |
| Upper Barnhart Lake..... | 7-3-53 | 26 | 7.9 | — | 12.4 | 200 |
| | 7-15-54 | 23.5 | 8.2 | 0.6 | 12.8 | 210 |
| | 7-18-55 | 27 | 8.2 | 0.6 | 12.2 | |
| | 8-8-55 | 24 | 8.3 | 0.4 | 13.1 | |
| Lower Barnhart Lake..... | 7-15-54 | 23 | 8.2 | 0.6 | 12.0 | 210 |
| | 7-18-55 | 27.5 | 8.4 | 0.6 | 12.1 | 210 |
| | 8-8-55 | 24 | 8.4 | 0.8 | 11.3 | |
| Outlet of Lower Barnhart L..... | 7-15-54 | 25 | 8.3 | 0.5 | 12.2 | 210 |
| McIntosh Lake..... | 7-3-53 | 22 | 7.8 | — | 13.8 | 240 |
| | 8-5-54 | 22 | 8.2 | 0.4 | 13.6 | 250 |
| | 7-18-55 | 27 | 8.4 | 1.1 | 13.1 | |
| Ocq. R., 0.5 mile above Falls..... | 8-1-55 | 29 | 8.4 | | | |
| Ocq. R., below Ocequeoc Falls..... | 6-30-53 | 23 | 8.1 | 0.3 | 13.3 | 225 |
| Southwest point of Ocequeoc Lake..... | 6-30-53 | 22.5 | 8.3 | 0.5 | 13.4 | 240 |
| | 5-9-54 | 20 | 7.8 | — | 12.8 | 225 |
| | 6-24-54 | 20 | 7.9 | — | 14.1 | 250 |
| | 10-10-54 | 11 | 7.8 | — | 14.0 | 250 |
| | 6-20-55 | 24.5 | 8.3 | | | |
| | 7-19-55 | 26 | 8.4 | 1.1 | 14.1 | |
| | 8-8-55 | 23 | 8.4 | 0.8 | 15.2 | |

TABLE 1. (Continued)

| Locality | Date | Water temp. °C. | pH | ALK. ¹ PPM. | | Cond. ² |
|---|----------|--------------------|-----|------------------------|------|--------------------|
| | | | | ph-th | M.O. | |
| Group Camp Bay of Ocequeoc Lake..... | 6-30-53 | 22 | 8.3 | 0.5 | 14.1 | 250 |
| | 6-24-54 | 20.5 | 8.0 | — | 14.1 | 250 |
| | 7-6-54 | 20.5 | 8.4 | 0.9 | 12.5 | 250 |
| | 10-10-54 | 11 | 7.8 | — | 14.1 | 250 |
| | 3-12-55 | 1 | 7.7 | — | 15.2 | 250 |
| | 6-20-55 | 25 | 8.3 | | | |
| | 7-19-55 | 26 | 8.4 | 1.1 | 13.5 | |
| | 8-8-55 | 22 | 8.3 | 0.6 | 15.0 | |
| | | | | | | |
| Ocequeoc River below Ocequeoc Lake..... | 5-9-54 | 8 | 7.8 | — | 12.4 | 225 |
| | 6-24-54 | 20.5 | 8.0 | — | 14.8 | 250 |
| | 7-19-55 | 25 | 8.4 | 1.0 | 13.2 | |
| | 8-8-55 | 22 | 8.3 | | | |
| Mud Lake..... | 6-30-53 | 25 | 7.9 | — | 11.8 | 195 |
| | 7-29-54 | 25 | 8.4 | 0.4 | 13.8 | 240 |
| Orchard Lake..... | 6-30-53 | 23 | 8.0 | 0.4 | 13.6 | 225 |
| | 7-29-54 | 26 | 8.4 | 0.5 | 14.3 | 250 |
| | 7-19-55 | 26.5 | 8.4 | 0.7 | 14.0 | |
| | 8-8-55 | 24.5 | 8.4 | 0.8 | 15.4 | |

¹ Alk. refers to alkalinity; ph-th to phenolphthalein alkalinity; M.O. to methyl orange alkalinity.

² Cond. refers to specific conductance expressed in reciprocal megohms.

thors distinguish the variety and comparisons cannot therefore be made with their work. The variety is so much larger and so abundant in this material that it was separated and its abundance recorded. The variety was sometimes more abundant at subsurface levels than at the surface, as, for example, at the 5 m level in the center and the western, isolated bay of Lake Nettie. This may indicate an adaptation or preference to colder water.

Keratella quadrata was numerically the most important rotifer in Allen's study (1920) of the San Joaquin River. Kofoid (1908) found it in the Illinois River as did Carlin (1943) in his study of the Motalaström. Although it is a common form in northern Europe, and Campbell (1941) reported it for Douglas Lake, Michigan, it was not present in any quantity in the Ocequeoc system. It appeared in fall and spring samples of the Lake Nettie region, with a maximum of 3/l, generally an average of less than 1. It was found in only one surface sample in Ocequeoc Lake (June 29, 1954) but in all except one of the 5 m samples from that lake, although in numbers consistently less than 1/l. It may be classed as a rare and cold-water form in this system.

Keratella serrulata was another species recorded in the Ocequeoc system. Ahlstrom (1943) states that it is, "A widely distributed species, rather common in some regions, almost absent from others. . . . Apparently most common in acid water, commonly found in sphagnum bogs." During this study it was collected in Lake Emma, the easternmost stream of the Floodwater and in Upper Barnhart Lake, in May 1953. In Ocequeoc Lake and the Lake Nettie region it was taken in May and October of most years. It was present as late as the last two weeks of June and

the first week in July in the Lake Nettie area in 1954 and also in the outlet of Ocqueoc Lake in June of that year. The population always was sparse, never reaching even 1/l. Hydrogen-ion concentrations, numerically below pH 7.0 were never recorded from these areas and perhaps limited the abundance and distribution of *K. serrulata*. From the evidence at hand, it appears to be another rare, and cold-water species in this system.

The genus *Polyarthra*, for purposes of this study, was divided into two groups, one with wide, serrated blades not greatly longer than the body (*P. euryptera*) and another with narrow, elongated, non-serrated appendages (*P. trigla*). The former group would include Carlin's (1943) *P. vulgaris*, *P. major*, *P. longiremis* and *P. euryptera*, while the latter would contain *P. dolichoptera*, *P. remata* and *P. minor*. More critical study of the population in this system is necessary to sub-divide the individuals into more than these two groups, and in 1953 even this division was not made. In Kofoid's work (1908) on the Illinois River, this genus was the second most abundant group of rotifers, perennial in occurrence, and exhibited both late spring-early summer and late summer-early fall pulses. Allen (1920) found the same abundance and cycles present in California and Carlin's *Polyarthra vulgaris* generally agrees in the periodicity of its pulses. Taking the genus as a whole, the largest pulse of this system occurred in early summer with several minor ones during the remainder of that season, at least for the two lakes sampled most frequently. This condition of small irregular pulses may result from the presence of several species (in the restricted sense) each reaching a peak at a different time. It is common for the *P. euryptera* group to be more abundant than the *P. trigla* forms in the Ocqueoc system.

Members of the *P. euryptera* group were frequently infested with organisms which coincide with Zacharias' (1902) "wurstförmigen Parasiten" and those mentioned by Holloway (1947). Budde (1927), in his study of rotifer parasites, places these parasites in the Class Sporozoa, with the name *Plistophora asperospora* Fritsch. Kofoid (1908) also found them ("Sporozoa") in the Illinois River. From quantitative records of 1954 the greatest infection was 16% of the individuals in samples taken July 19 at the outlet of Lake Nettie. The middle portion of the lake showed a 12% infection and the area of the 1939 Dam 14% for the same date. The individuals in this area were parasitized more than in the other lakes. The parasites appeared in June and continued to be present through October, infecting an overall average of 4% of the population.

Another parasite was found in considerable numbers in *Polyarthra* in the October 10 collection of 1953. It was determined by Dr. Robert A. Paterson to be a species of *Olpidium*, an aquatic phycomyete of the group Chytridiales. The parasite occurred in other lakes and other collections of 1953 but was most abundant in October of that year in the Lake Nettie area. An average infection of 2.5% occurred in that

lake during 1954. How effective the two parasites were in reducing the population of *Polyarthra* is not known, but the time of highest infection with *Plistophora asperospora* was also the time of lowest population in Lake Nettie in 1954.

The genus *Synchaeta*, which was the most abundant rotifer in the Illinois studies (Kofoid 1908), was variable in its distribution in the Ocqueoc system and seldom reached a great abundance. Of the species present, *Synchaeta stylata* was generally the most common. The genus was virtually absent in some lakes and reached its maximum only in the larger bodies of water. In Ocqueoc Lake, the three larger species, *S. stylata*, *S. longipes* and *S. oblonga* combined to form an early summer pulse of less than 300 individuals per liter. In Lake Nettie a different condition existed with summer minima of these species and apparent fall and spring maxima. A situation similar to the latter was reported in the studies of Kofoid (1908) and of Allen (1920). Carlin (1943) found one species with a winter, and four with summer, pulses, although the whole group was not abundant. He also classed *S. kitna* as rare in the Swedish stream which he studied. Other authors do not mention this latter species in their river studies. In the Ocqueoc system, *Synchaeta kitna* was generally found in lakes where other species of the genus were present but in number less than 10/l. An exception to this was in Ocqueoc Lake where an August pulse produced numbers in excess of 700/l, and in fact this species was responsible for the August pulse of total plankton. Members of the genus *Synchaeta* are also susceptible to parasitic infection, mostly of the sporozoan type. Only a few infected individuals containing *Olpidium* were discovered in the collections of August 1954, from Lake Nettie. On the other hand, that lake contained the majority of rotifers parasitized by sporozoans and this averaged about a 7% infection. The period of infestation occurred in June and July and was almost exclusively confined to *Synchaeta stylata*.

The genus *Brachionus* was practically absent from the collections of this system. Kofoid (1908), in his Illinois River studies, estimated this genus as about 25% of the Order Ploima, which contains most of the limnetic genera. Allen (1920) found it in large numbers in the San Joaquin and, although rotifers were not abundant in the Upper Mississippi, Galtsoff (1924) recorded this genus as the most prominent one. Ahlstrom (1940) makes the following remarks in monographing the group: "The genus *Brachionus* is world-wide in distribution. However, it is not 'cosmopolitan' as it is confined to waters with a hydrogen-ion concentration above pH 6.6. It is entirely absent from acid water. Some species of *Brachionus* are very widely distributed, being found in all parts of the world in favorable habitats. . . . Other species are found in many parts of the world but less commonly. . . . Some species seem to have a definitely localized distribution. . . . A number of species of *Brachionus* have been found in very few habitats." In view of the variety of habitats with alkaline wa-

ters in the Oquee system, it is indeed remarkable that the genus does not appear more frequently and in greater abundance. Scattered individuals, less than 1/l, occurred in spring, autumn, or winter samples from Lake Nettie, Oquee Lake or the river above or below these areas. Only twice were individuals found on other dates.

Other genera appeared in various collections from the different localities sampled but were not present in sufficiently large numbers or with any regularity to warrant a detailed discussion here. Their presence has been pointed out previously.

The lotic situations in this system do not generally maintain a rate of rotifer production sufficient to keep pace with the straining action of the plants and the periphyton. Consequently, where a sufficient length of continuous stream exists, all plankters are removed. In comparison to the much larger Illinois and San Joaquin Rivers, the running water of the Oquee is not very productive, and, as a matter of fact, almost all plankton found in this river comes originally from lakes of the system. A few non-limnetic forms appear in collections but they have undoubtedly been washed from the periphyton or swept up from the bottom. Although no lakes occur along its course, the Hocking River in Ohio (Roach 1932) with a drainage area of 1,200 sq mi developed an average planktonic rotifer fauna, over its entire course, of 314 individuals/l. We must conclude that the actual running water of the Oquee is less productive than that of most other rivers, which is undoubtedly due to its small size (about 100 square mile area of drainage), its young state, geologically speaking, and its overall fast current. Plankton production in lakes of this system, however, does compare favorably with that of other lakes, and even surpasses them in some instances. Moreover, if the lotic areas were of a greater volume and depth, and the current was sufficiently slow, there is nothing inherent about the water of the Oquee River that would not permit it to produce a planktonic rotifer assemblage quantitatively equal to that of the larger rivers with which it has been compared.

SUMMARY

The objectives of this study were: (a) comparison of the qualitative and quantitative aspects of the separate rotifer faunas in each of the discrete lotic and lentic habitats of the Oquee River system; (b) analysis of the differential effects of stream and impoundment conditions, natural or otherwise, on both autochthonous and allochthonous rotiferan faunas; and (c) determination of those factors, whether physical, chemical, biological or combinations thereof, which might be responsible for the development and maintenance of any autochthonous rotifer fauna in the system.

The investigation was carried on from 1952 through the summer of 1955. Both living and preserved plankton samples were examined and preserved samples totaled 534 from 42 field stations

throughout the system. Quantitative samples were obtained from all significant lakes and from 23 stations in the river. The Lake Nettie and Oquee Lake areas were sites of more detailed study. Selected physico-chemical data were taken simultaneously with plankton collections.

Lakes and artificial impoundments of the system were the major locations of plankton development. Lotic situations did not possess a planktonic rotifer fauna distinct from the lakes. Rather, most of the plankton was derived from the lakes, decreased in quantity downstream from the lakes and eventually disappeared. The rate of removal of the plankton was related to length of stream segment, current, depth of water, turbulence, and amount of vegetation or other objects in the channel which supported a periphyton assemblage. The vegetation and periphyton exerted a pronounced filtering effect on the plankton and very little was transported from one lake to another by the river.

Twenty-four genera containing 34 species of rotifers were identified in the plankton. The majority of them have been reported in studies of other lakes and rivers. The rotifer fauna varied somewhat from lake to lake, but the variation was more quantitative than qualitative in nature. Within a single lake considerable quantitative variation also occurred. The largest number of species was present in Lake Nettie but the total population there was not the largest within the system. Oquee Lake produced the greatest quantity of plankton.

Males of *Keratella cochlearis* were present in autumn collections from Lake Nettie and Oquee Lake and in summer collections of Moore's Lake. The unusual presence of males in summer collections has been related not to temperature, but to abundance and quality of food material and to conditions of crowding within Moore's Lake. *Limnias ceratophylli* was found as a member of the plankton in considerable numbers in a few lakes of the central lake region. It has previously been regarded as a sessile species and is not usually found as a member of the plankton community. The genus *Brachionus* was virtually absent from the entire system in spite of the alkaline character of the water. *Keratella*, *Polyarthra* and *Synchaeta* were the genera occurring in greatest abundance during most of the year and throughout most of the system. *Keratella cochlearis* was the dominant species for the system, both in abundance and distribution.

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ECOLOGY AND EVOLUTION IN ISLAND POPULATIONS OF SALAMANDERS IN THE SAN FRANCISCO BAY REGION

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INTRODUCTION

Studies of the striking results of evolutionary processes operating in island populations have made possible important contributions to biological theory. While the phenomenon of morphological differentiation on islands has been well established by these studies, very little is known of the processes which bring it about. Isolation does not, of itself, account for the rapidity with which new genotypes develop or for the particular course the development takes. It appears, rather, that isolation permits the operation of mechanisms more immediately concerned in the development of divergence. This study was undertaken in the hope of identifying mechanisms of possible evolutionary significance at work in salamander populations of islands in the area of San Francisco Bay. Primary emphasis was placed on the clarification of the role of ecological factors. The intent was to review the broader characteristics of the island environments as they might be related to evolution of the salamanders and to follow this with a comparative study of dynamics in island and mainland populations. Finally, patterns of morphological variation were investigated and their possible correlation with zoogeographic and ecologic factors was considered.

The distribution of the populations studied is shown in Fig. 1. Island populations of the Arboreal Salamander, *Aneides lugubris*, were studied on South Farallon Island in the Pacific Ocean west of San Francisco and on Red Rock in San Francisco Bay. Mainland populations were studied on the Marin Peninsula on the west side of the bay and at Point Richmond on the east side. Island populations of the California Slender Salamander, *Batrachoseps*

attenuatus, were studied on Red Rock, Yerba Buena, Brooks Island, Angel Island, East Marin Island and West Marin Island, all in San Francisco Bay. Mainland populations of both species were studied on the Marin Peninsula and at San Mateo on the west side of the bay, at Sonoma at the north end, and at Pt. Richmond and Berkeley on the east.

Thanks are due the following organizations and persons for permission to visit the various islands: U. S. Army Corps of Engineers, U. S. Dept. Interior, U. S. Coast Guard, Mr. Thomas B. Crowley, Mrs. Christine Rogers, and Mr. Charles C. Harlan. I am particularly indebted to the U. S. Coast Guard for transportation to South Farallon Island and for the use of Coast Guard facilities there. Visits to the bay islands were made possible by the loan of a motorboat from the Department of Zoology, University of California, which also provided storeroom supplies. Many friends, especially Paul Marhenke, aided in field work. Alan E. Leviton, California Academy of Sciences, facilitated my check of the Academy collections for herpetological material from the islands. This study was supported by a grant from the University of California Graduate Student Research Fund and was the basis of a doctoral dissertation. I am indebted to the following members of my committee: R. C. Stebbins, J. E. Davis, and G. L. Stebbins. W. Z. Lidicker, Museum of Vertebrate Zoology, gave additional criticism and suggestions.

SPECIES STUDIED

Amphibians are favorable forms for population studies in that large numbers are often easily collected and preserved. The relatively high efficiency of salt water as a barrier to amphibians permits a considerable degree of isolation on islands only a

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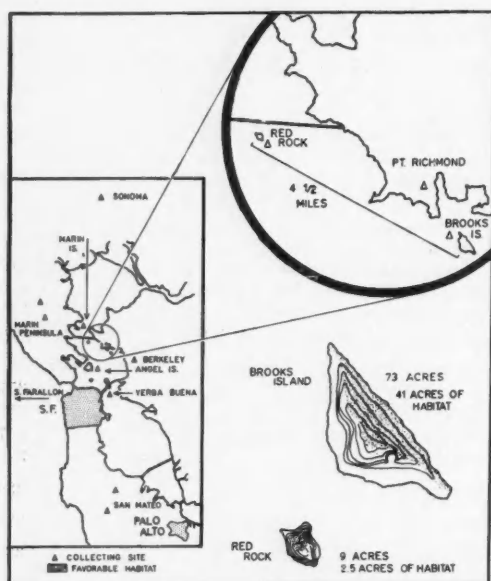


Fig. 1. Location of islands and of mainland sampling areas in the San Francisco Bay region. Shading indicates distribution of favorable habitat on Brooks Island and Red Rock. Upper right inset shows relationship of these two islands to the Point Richmond land mass.

short distance from the mainland. The availability of information on mainland patterns of variation, basic life history, and ecology was also important in the choice of the species studied.

The California Slender Salamander, *Batrachoseps attenuatus*, ranges from Oregon to Baja California (Stebbins 1951). Variation has been studied by Hendrickson (1954) who considered the large southern California form, *pacificus*, to be a subspecies of *attenuatus*. He thus recognized only two subspecies, *pacificus* and *attenuatus*, and he felt that over most of its range *attenuatus* was composed of partially isolated and moderately variable local populations. He noted no pattern of variation associated with San Francisco Bay. *Batrachoseps* is found in moist situations under large objects and in surface litter in chaparral, grassland, moist coniferous forest and coniferous forest biomes. Its food habits are unspecialized. Food items listed by Stebbins (1951) are, "Earthworms, small slugs and many kinds of small terrestrial arthropods such as sowbugs, millipedes, and insects, including collembolans, aphids, caterpillars, small beetles (weevils, etc.), beetle larvae, and ants." Individuals are active on the surface during the moist season of the year, but retreat into crevices and burrows during dry weather. Hendrickson (1954) found some correspondence between abundance on the surface and rainfall. December, January, February and March were found by him to be the months of greatest surface abundance.

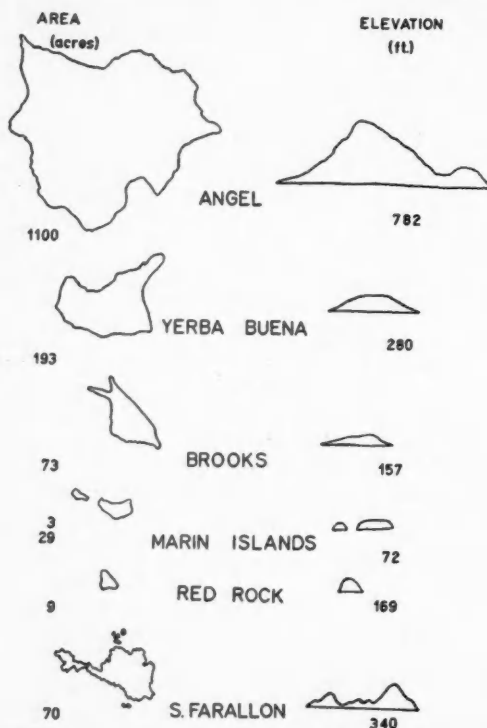


Fig. 2. Area and topography of islands studied in the San Francisco Bay region. Profiles are through the long axis of each island.

When the animals appear on the surface following the first fall rains, females are gravid and most appear to carry sperm stored from mating which has taken place previously. Most females deposit their eggs in a moist location within two weeks of their appearance on the surface. The eggs are not tended by adult salamanders.

The Arboreal Salamander, *Aneides lugubris*, ranges from Humboldt to San Diego counties in the California Coast Range and occurs in Calaveras and Madera counties in the Sierra Nevada foothills. No study of variation throughout its range has been published. Populations on the mainland surrounding San Francisco Bay appear to be homogeneous. A sharp line of morphological change occurs along the Salinas Valley to the south (Stebbins 1954). The Farallon population has been described as a subspecies, *Aneides lugubris farallonensis*, by Van Denburgh (1905). Habitat of *Aneides lugubris* is similar to that of *Batrachoseps* although individuals are frequently found in situations drier than those typical of the latter. While *Aneides* is a good climber and is occasionally found in cavities in trees, it is by no means limited to arboreal habitats. Rosenthal (1957) correlates the distribution of this salamander with that of the oaks *Quercus agrifolia* and *Quercus wislizenii*, but concludes that this may be the result

TABLE 1. Distribution of plant associations inhabited by *Batrachoseps* and *Aneides*, San Francisco Bay region.

| Island | Grass-land | Subur-ban | Euca-lyptus | <i>Baccharis</i> -grassland | <i>Baccharis</i> -Lupin | Broad sclero-phyll | Farallon Weed | Description |
|-------------------|------------|-----------|--------------|-----------------------------|-------------------------|--------------------|---------------|--|
| Yerba Buena | | X | X | | | | | Former vegetation apparently broad sclerophyll on N and E slopes, chaparral and grassland on the S and W. The island now intensively suburbanized. |
| Brooks Island | X | | | X | | | | Grazing has probably altered the vegetation in favor of grassland. The summit and the S and W slopes are grassy. Grass merges with open <i>Baccharis</i> stands and occasional Buckeye on the N and E slopes. |
| Red Rock | X | | | | X | | | Appears essentially unaltered. S and W slopes dry and rocky with sparse grass which becomes denser toward the summit where small areas of turf are found. N and E slopes have a <i>Baccharis</i> and lupin cover. |
| East Marin Island | X | | X open stand | | | X | | Remnants of well developed broad sclerophyll on the N side. Considerable alteration has resulted from landscaping activity. |
| West Marin Island | | | | | | X | | Unaltered by man, but influenced by the egret rookery utilizing the broad sclerophyll on N side where guano deposits kill off most undergrowth. Chaparral on S side, predominantly <i>Rhus diversiloba</i> and <i>Photinia arbutifolia</i> . |
| Angel Island | X | X | X | X | | X | | Upper slopes with grassland and open chaparral merging into dense chaparral and broad sclerophyll on canyon slopes beneath. Suburbanized areas scattered, often overgrown with chaparral or tall grasses. Several dense eucalyptus stands. |
| Farallon Island | X | | | | | | X | Low herbaceous vegetation only, no trees or shrubs. |
| Mainland | X | X | X | X | X | X | | Additional habitats: Redwood and redwood-border forests. |

of response to the same complex of climatic and edaphic factors. Zweifel (1949) reported beetles, caterpillars, isopods, centipedes and ants as important food items. Stebbins (1951) noted that *Batrachoseps* are taken. The period of surface activity is the same as that for *Batrachoseps* in the San Francisco Bay area (Rosenthal 1957) but eggs are deposited at the end of this period (June, July) rather than at the beginning. Stebbins (1954) reports that the eggs are deposited in clusters of 12-18. Ovaries of individuals examined in the present study contained 5-26 maturing oocytes. Eggs and recently hatched young are attended by adults. Young first appear at the surface in early fall. They may disperse or remain for a time in groups associated with one or two adults.

ISLANDS STUDIED

The locations, area, and topographies of the islands investigated are shown in Figs. 1 and 2. The

plant associations are described briefly in Table 1. The occurrence of non-avian, non-marine vertebrates is summarized in Table 2. Of the 7 islands investigated, Red Rock, Brooks Island, and South Farallon received concentrated attention and will be considered in greater detail in the following discussion.

All of the islands are rocky, and soil is sparse on the steeper slopes. Angel Island, largest of the group, is dissected by steeply sloping canyons leading to rocky beaches. There are no permanent bodies of water, but streamlets flow in the larger canyons throughout most of the year. There has been extensive human occupancy, including a military base and hospital and an immigration station. Most of the formerly suburbanized area has been abandoned and only a small military detachment is now present. The area of the former hospital is being developed as a state park. Planting of trees and shrubs has been extensive. While the

TABLE 2. Distribution of non-avian, non-marine vertebrates on islands of the San Francisco Bay region.

| Species | ISLAND | | | | | | |
|---|--------|-------------|-------------|--------|----------|----------|----------|
| | Angel | Yerba Buena | S. Farallon | Brooks | E. Marin | Red Rock | W. Marin |
| <i>Oryzotylagus cuniculus</i> | | | X | | | | |
| <i>Microtus californicus</i> | X | | | | | | |
| <i>Rattus norvegicus</i> | | | | X | X | | X |
| <i>Mus musculus</i> | | | | X | | | |
| <i>Odocoileus hemionus</i> | X | | | | | | |
| <i>Scapanus latimanus</i> | X | | | | | | |
| <i>Thamnophis elegans</i> | X | | | X | | | |
| <i>Coluber constrictor</i> | X | | | | | | |
| <i>Sceloporus occidentalis</i> | X | | | | X | | |
| <i>Gerrhonotus coeruleus</i> | X | X | | X | | | |
| <i>Gerrhonotus multicarinatus</i> | X | | | | | | |
| <i>Batrachoseps attenuatus</i> | X | X | | X | X | X | X |
| <i>Aneides lugubris</i> | X | | X | X | | X | |

island probably was occupied by aborigines, subsequent occupancy has been sufficient to erase any obvious signs of encampments. Ten species of non-avian vertebrates have been recorded on the island (Table 2).

The topography of Yerba Buena is less dissected. There are no streams or ponds, but considerable moisture is locally available as lawns and gardens are irrigated during the dry season. Naval and Coast Guard installations occupy a large part of the island and the remainder is taken up with the homes of military personnel. There has been and continues to be much landscaping activity with consequent opportunity for the introduction of salamanders.

The northern and eastern slopes of Brooks Island are gently sloping while those to the south and west are steeper and have been altered by quarrying operations. The most extensive quarrying, on the southwest corner of the island, has produced a broad bench with many irregularities resulting from overgrown rock dumps and littered with rocks, planks, and abandoned equipment. Three of the larger and deeper depressions in this area contain freshwater pools throughout the year. The southern and western slopes are very dry and rocky, the northern and eastern slopes are moist with a well developed turf and occasional rock outcrops. To the northwest a long low spit of land has been created by dredging operations. The island was used for grazing at about the turn of the century and the foundations of small ranch buildings remain. Large midden heaps indicate extensive aboriginal use. The quarries are abandoned and at present the island is visited only by occasional hunters and fishermen. Brooks Island is separated by 800 yds of water from the southern tip of Point Richmond and by 2500 yds from the mainland to the east. The basin between the island and the mainland is filling with sediment and water depths are only 3-4 ft at low tide except where deeper channels are maintained by dredging. The vegetation on Brooks Island is variously modified grassland. On the northeast slopes are areas of open shrub (*Baccharis*)—grassland with about a dozen buckeye (*Aesculus*) trees on the sites of the Indian

middens. Vegetation on the southern and western slopes has been altered by the quarrying operations and shows the effects of sparse soil and reduced moisture but is similar in aspect to the rest of the island. As is indicated in Fig. 3, the *Baccharis*-grassland is rich in plant species, in fact it appears to be richer than a similar mainland area. This may be due to the lack of recent grazing activity and the infrequency of fires (the island was burned in October, 1956, but apparently there had been no burning for many years previous to that time). The vertebrates found resident on Brooks Island at the time of this study were: *Batrachoseps attenuatus*, which is abundant on the north and east sides, and rare on the south and west, *Aneides lugubris*, a small population of which was discovered in the quarry dumps at the southwest corner at the conclusion of the study, *Gerrhonotus coeruleus*, also found in the latter area, *Thamnophis elegans* (ssp. *terrestris*?), *Rattus norvegicus* and *Mus musculus*, both abundant, the Red-winged Blackbird, *Agelaius phoeniceus*, Western Meadowlark, *Sturnella neglecta*, and the Song Sparrow, *Melospiza melodia*. The invertebrate fauna, like the flora, seems rich in number of species, approximating or exceeding that of a similar mainland habitat (Fig. 3).

The two Marin Islands are plateaus with precipitous sides dropping into the water or to narrow rocky beaches. East Marin has remnants of a well developed broad sclerophyll forest along the northern side of the island which slopes northward and is thus more protected from desiccation. The island is currently used as a country estate and there has been a moderate amount of landscaping and planting, modifying but not destroying the native vegetation. Quarrying operations on the southern side have produced a small, brackish pond separated from the bay by a narrow strip of beach. *Rattus norvegicus* has a foothold on the island and periodic poisoning operations aimed at rat control may have eliminated the native rodent population if one existed. *Batrachoseps* is common and there is a small population of *Sceloporus occidentalis*. A large shell heap at the western end attests to extended aboriginal occupation. West

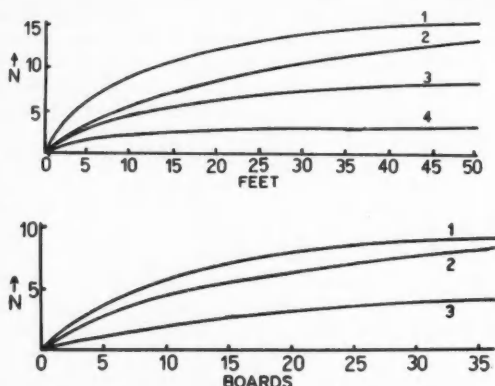


Fig. 3. Indices of biotic complexity on islands and mainland in the San Francisco Bay region. Upper set of curves represents floral diversity as indicated by species-distance curves based on counts of species along the following 50-ft line transects: 1, shrub (*Baccharis*)-grassland, Brooks Island (average of 3 transects); 2, *Baccharis*-grassland, mainland (average of 3 transects); 3, *Baccharis*-grassland, Red Rock (average of 4 transects); 4, *Baeria*-grass association, South Farallon Island (average of 7 transects). Lower set of curves represents faunal diversity indicated by counts of invertebrate types (arachnids and isopods were each considered a type; other groups were recorded by species) found beneath boards used in sampling salamander populations: 1, Brooks Island (average of 3 visits); 2, mainland (average of 3 visits); 3, Red Rock (average of 3 visits). Corresponding floral and faunal counts were made in the same areas; N = no. of plant species or invertebrate types.

Marin has a gently rounded summit with oaks covering the more extensive northern slopes. Intensive use of these trees by nesting egrets has led to the accumulation of guano deposits which have prevented the development of undergrowth. On the crest of the island and its southern exposure are patches of *Photinia* and *Rhus* interspersed with small grassy glades. Collecting revealed a few *Batrachoseps*, but no other amphibians or reptiles. Mammal sign indicated the presence of one or two *Rattus norvegicus* and of a smaller rodent, possibly *Reithrodontomys* or *Mus*.

Red Rock is a round-topped island with precipitous sides. On the south and west the rounded summit is cut by cliffs dropping to the narrow beach of coarse angular gravel. On the north, steep slopes of loose soil reach down almost to the beach. On the eastern side a break in the cliffs permits the visitor to climb a steep path to a cirque-like bowl with a floor of talus intermixed with soil and overgrown with vegetation. The path leads from this bowl to the summit along a steep shoulder. The soil on Red Rock is poorly developed with much angular rock and gravel mixed with finer materials. There is little humus. The vegetation in 1956-57 was dominated by a shrubby species of *Lupinus*. This died off during the summer of 1957 and in the 1957-58

season lupin was no longer important in the association. The dominant shrub on the moister north and east slopes is now *Baccharis*. There is no evidence of extended human occupation of Red Rock at any time, but several tunnels and trenches on the western side record limited attempts to mine cinnabar ore there. The island is 5000 yds from Point San Quentin to the west and 2000 yds from Point Richmond to the east. There is a marked reduction in number of species in the biota of Red Rock as compared with Brooks Island and the mainland (Fig. 3, Tables 1 and 2), probably due in large measure to the island's small size and edaphic restrictions. Three species of vertebrates are resident: *Batrachoseps attenuatus*, *Aneides lugubris*, and the Song Sparrow, *Melospiza melodia*. *Rattus norvegicus* was reported to be abundant in 1934 (Museum of Vertebrate Zoology specimen nos. 63287-89), but no mammals are found on the island at present.

The Farallon Islands are elevated portions of a submarine ridge running southwest from the vicinity of Point Reyes on the coast north of San Francisco Bay (Hanna 1951). The rocks are primarily granitic. North and Middle Farallon appear to have little or no soil and are not known to support any non-maritime vertebrates. South Farallon, located 27 mi west-southwest of the Golden Gate is about 0.75 mi long, with a shoreline deeply cut by surge channels. One of these divides the island in half at high tide. There is a series of rocky crags, some with sheer cliffs dropping into the sea on one or two sides. Along the southwest side there is a broad wave-cut bench (Hanna 1951) about 50 ft above present sea level. On the lower and less precipitous slopes guano-enriched earth has filled the spaces between the rocks, and on the level bench soil is well developed to a depth of a foot or more between the abundant boulders. There is no standing or running fresh water with the exception of seepage areas on the cliffs and beneath the water tanks of the Coast Guard installation. Beach areas where driftwood can lodge are small and few in number and accumulations of flotsam were found at only two points on the island. Burrows of petrels, auklets, and rabbits riddle the soil and, with the many boulders, provide abundant cover for salamanders. Water depths between the island and the mainland do not exceed 180 ft but a few thousand yards to the west the continental shelf drops off sharply. With the exception of one cypress tree planted beside Coast Guard buildings the vegetation is herbaceous. *Baeria maritima* is the dominant species. In protected areas nearly pure stands of dense low grasses may be found. During the summer months the island becomes very dry and its appearance is almost desert-like. Despite the relatively large size of the island, the biota is limited. Species of plants (Fig. 3) and invertebrates are few. There is a single resident land bird, the Rock Wren, *Salpinctes obsoletus*. The only terrestrial mammal is the European Rabbit, *Oryctolagus cuniculus*, introduced sometime prior to 1870 (Hanna 1951). This

species is noted for its ability to alter the vegetation. Whether it has had such an effect on South Farallon is unknown. There are no records of reptiles from the island. *Aneides lugubris* is the only amphibian. Evidence of aboriginal human occupation has not been reported. The island was once a base for Russian seal and other hunters and was an important source of eggs for San Francisco in goldrush days. The lighthouse was built shortly after 1850, and personnel connected with its operation have occupied the island since that time. The earliest collection of *Aneides* listed by Van Denburgh (1905) was made in 1896. Unsuccessful attempts to establish trees or shrubs could have led to the introduction of *Aneides* prior to this time, but there is no evidence to support this suggestion.

ISLAND COMMUNITIES

The restricted nature of island floras and faunas is amply illustrated in the literature of biogeography, but little has been said of the shifts in community structure which must result. Impoverishment of the biota stems from the interaction of isolation, restricted area, and climate. Restricted area may limit topographic and edaphic diversity and many species and associations may thus be excluded. Space requirements of larger animals may prevent the development of self-perpetuating populations of these species. Absence of niches dependent on the existence of larger species would in turn prevent the survival of some smaller forms. The effects of isolation on the community will be most marked where islands have been populated by waifs and many species have been excluded by the combination of chance and rigid selection involved in the waiving processes. Small islands in the open sea may be exposed to severe climatic conditions during stormy weather and thus be uninhabitable to species that could survive readily if the island were in a protected bay. The overall result of the interactions of these factors appears to be a striking simplification of the ecosystem.

Despite their proximity to the mainland a simplification such as that postulated above was indicated in the islands studied. In biotic terms the effect may be expressed as a reduction in the number of associations represented (Table 1), and in the number of species in any single association (Fig. 3).

The expression of ecological simplification may be modified by special conditions. On the basis of Fig. 3 the shrub-grassland on Brooks Island appears to be richer in species than is an apparently comparable community on the mainland. As has been suggested, this may be the result of protection from fire and grazing. Red Rock, located nearby and similarly isolated, shows a relative reduction in species number, probably due to smaller size and unfavorable topography. South Farallon, almost identical in area with Brooks Island, has a flora even more impoverished than that on Red Rock. This may result both from greater isolation and from the activities of nesting sea-birds. Effects on plant communities of

trampling and guano deposition by island-nesting marine birds have been demonstrated by Gilham (1956, 1956a). The egret colony on West Marin Island provides a further example of how the activities of organisms already present may have tended to limit ecological complexity.

Similar shifts in community complexity are indicated in Fig. 3 for invertebrate faunas. The data utilized in the curves were obtained by recording the macroscopic invertebrates observed beneath 12-inch squares of board used in sampling salamander populations and indicate relative diversity only. On South Farallon time limits made this technique impractical, but records of invertebrates found along the vegetational transects indicated restriction of the invertebrate fauna to the point where less than a dozen species provided most of the invertebrate biomass.

That the simplification of the ecosystem affects individual species may be most readily illustrated in terms of such relationships as food habits and predation. In a comparative study of food habits, stomach contents of 27 adult and subadult *Aneides* from Red Rock and 27 individuals of similar size from South Farallon were examined. Contents of the 27 stomachs from each locality were placed in petri dishes and sorted under a dissecting microscope. Food items were sorted as "types," a designation under which insect species were sorted separately, but spiders and isopods were each considered a "type." The stomachs of the Red Rock animal contained 42 items among which 21 types were recognized, while the stomachs of the South Farallon sample contained 77 items among which only 12 types were represented, reflecting the simplification of the ecosystem indicated by the observations on floral and faunal diversity.

Reduction in the complexity of predation on an individual species can also be illustrated in the island populations. On the mainland around San Francisco Bay are found at least 10 species of vertebrates which are known to prey on *Batrachoseps* in the wild or have been observed to eat *Batrachoseps* in captivity. Only 4 such species have been recorded from Brooks Island and only 1 from Red Rock. A similar list might be compiled for *Aneides* in which Red Rock and South Farallon would represent the final stage where no known or potential predators appear to exist (gulls would undoubtedly take salamanders active in the daytime, but since the species studied here are nocturnal the opportunity for such avian predation is believed to be inconsequential).

The effect of reduction in the number of prey-predator relationships entered into by a species may be quantitative (lessening of predator pressure) or qualitative. Rand (1954) has attempted to correlate increased variability in an island lizard population with a decrease in the proportion of individuals with regenerated tails. This latter proportion is taken as an index of predation. While his mainland sample was too small (8 individuals) for his results to be significant, his suggestion that the proportion of

animals with lost or regenerated body parts may be used as an index of autotomy-inducing predation is valuable and is applied to the analysis of predation on *Batrachoseps* in the present study. In *Batrachoseps*, tail regeneration may be recognized with certainty in its earlier stages but may be obscured later. In cases where regeneration has progressed for a time, but is still clearly recognizable, it can be shown that fully formed vertebrae are present in the regenerated portion. Pigmentation of regenerated parts eventually becomes normal, and regeneration must, therefore, become undetectable. For the purpose of comparison of predation in different samples this transition may be ignored if all samples receive the same treatment and only clearly recognizable regeneration is recorded. Table 3 shows the proportion of regenerated tails found in island and mainland samples taken in November and December. In terms of quantitative reduction of predator pressure as indicated by autotomy there is no significant difference between the islands as a group and the mainland average as tested by the chi squared method. Red Rock seems to be a special case. *Aneides* is the only known or potential predator present. It appears that salamanders depend to a large extent on motion for location and recognition of their prey, and that against such a predator autotomy would be effective. It is possible that on Red Rock predation by *Aneides* on *Batrachoseps* is more effective on tails and less so on whole animals. This suggests that caution must be used in accepting the frequency of regenerated tails as a quantitative index of predation.

The preceding paragraphs have demonstrated the simplification of island ecosystems and the effect of this simplification on the resident salamanders in at least two ways. These simplified environmental relationships necessarily have a bearing upon the intensity and focus of natural selection, and the direct evolutionary implications of this will be taken up in the discussion after some of the ecologic consequences have been considered.

ORIGIN OF THE ISLAND SALAMANDER POPULATIONS

In the interpretation of both ecological and morphological variation it is important to be able to refer to the span of time over which adjustment to the island environments may have taken place. The way in which the population became established is also of interest since it can be of considerable importance in determining subsequent events. Ecological and genetic situations of a segment of an established mainland population which has been isolated by rising waters are quite different from those of a population originating through the arrival of one or a few waifs in a hitherto unpopulated area.

GEOLOGIC BACKGROUND

Howard (1951) has outlined the development of San Francisco Bay. The coast ranges emerged at about the middle of the Miocene. In the Pliocene the sea penetrated through the Salinas Valley, 70 mi

TABLE 3. Frequency of regenerated tails in island and mainland populations of *Batrachoseps*, San Francisco Bay region.

| Locality | No. of Animals | Percentage with regenerated tails |
|-------------------------|----------------|-----------------------------------|
| Berkeley..... | 69 | 7% |
| Marin Peninsula I..... | 55 | 16% |
| Marin Peninsula II..... | 26 | 19% |
| E. Marin Island..... | 34 | 0% |
| Brooks Island..... | 106 | 3% |
| Red Rock..... | 65 | 32% |

south of San Francisco, and entered the San Joaquin Valley behind the coast ranges. The sea receded from this area with the uplifting of the coast range region in mid-Pliocene. The drainage of the Sacramento River and other rivers in the San Joaquin Valley appears to have been established in its present form at this time. In the middle Pleistocene there was a major re-elevation of the coast range, including the Marin and Berkeley hills. Through the rising lands the Sacramento River carved the valley of the present day. Along the course of this valley were hills which were later to become islands. At the end of the Pleistocene the flooding of this river valley to form the bay and isolate the islands occurred.

There is some disagreement as to whether the change in relative levels of land and water at the time the bay was flooded was due in part to subsidence of the land (Howard 1951) or entirely to post-Pleistocene sea level rise (Louderbach 1951). In either case the resulting isolation would have been the same, but the time schedule for isolation would probably have differed if land movements were involved. Louderbach (1951) estimates that flooding of the bay by the sea began 15,000-25,000 yrs ago and proceeded at the rate of 0.25 in/yr. Recent radio-carbon dating of the eustatic sea level changes of the Pleistocene (Godwin, Suggate & Willis 1958) indicates that the sea rose at a rate of 0.36 in/yr between 14,000 and 6,000 yrs ago and reached its present levels 5,500 yrs ago. Thus the latter date may be taken as the minimum age for the bay islands. Beyond that time isolation of each island would have been regulated by bottom contours between it and the mainland and by any land movements that may have occurred. The maximum period of isolation of any of the islands is probably less than 10,000 yrs.

Since the flooding of the bay, deposition of sediments has built towards new connections of the islands with the mainland. Recent human activity has directly and indirectly hastened this process. The low range of hills which forms Point Richmond (Fig. 1) is now broadly connected with the mainland, but the United States Geological Survey topographic maps made in 1915 show only a very narrow strip of low ground connecting it to the mainland across a broad strip of salt marsh. It therefore appears

that the Point Richmond land mass was an island until recent times.

There seems to be no indication in the geological literature of the age of South Farallon Island or of possible connections with past land masses. The high wave-cut benches and sea caves found on the island are not matched along the shores of San Francisco Bay and a somewhat different history is thus suggested. Since maximum water depth between the island and the mainland is 180 ft, sea level change could have isolated the area about 11,000 yrs ago if there were no complicating land movements.

ZOOGEOGRAPHIC CONSIDERATIONS

Studies of variation by several authors have indicated that the bay has been an important factor in speciation for birds and mammals but has had relatively little effect on patterns of variation in amphibians and reptiles. Effects of the bay on speciation have been recorded in Song Sparrows (Marshall 1948), shrews (Rudd 1955), and rodents (Hooper 1944). Reference to Stebbins' (1954) distribution maps shows that among amphibians and reptiles the bay appears to separate sub-species only in two species of snakes (*Thamnophis sirtalis* and the aquatic group of *Thamnophis elegans*). East of the bay the Sacramento River serves as a barrier to lizards whose distributions are primarily southern, but there is no evidence of speciation resulting from the bay's formation. While the distributions and variation patterns of amphibians take little cognizance of the bay they are markedly affected by the Salinas Valley which is now a minor barrier, but was the site of the seaway into the San Joaquin Valley in the Pliocene. Three northern salamander species, *Taricha granulosa*, *Dicamptodon ensatus*, and *Aneides flavipunctatus*, span the bay with no recognized variation, only to reach the southern limit of their distributions abruptly at the edge of the Salinas Valley. Three other species, *Ensatina eschscholtzi*, (Stebbins 1954), *Batrachoseps attenuatus*, (Hendrickson 1954), and *Aneides lugubris*, (Stebbins 1954), whose distributions cross both areas show little or no variation across the Golden Gate, but marked divergence across the Salinas trough. These data suggest that the salamanders were on the scene in the early Pliocene and that the patterns of variation established at that time have changed little in the intervening period. The existence of *Batrachoseps* in the Pliocene has been established by Peabody's (1940) study of trackways. The conclusions suggested by the fossil evidence and the variation and distribution patterns are that populations of the salamanders studied may have been present in the area when the bay was formed, that they could have been isolated at that time, and that a conservative evolutionary response to geographic barriers is indicated by the contrasting patterns of amphibian and mammal variation about the bay.

Native mammals are established only on Angel Island and the representation is very poor (Table 2). Of 9 species of small rodents occurring on the

nearby Marin Peninsula only *Microtus californicus* occurs on Angel Island, and of 4 insectivores, only *Scapanus latimanus* (described as an endemic subspecies by Palmer 1937) has been reported. *Mus* and *Rattus* have established successful populations on Brooks Island, and *Rattus* is present on both Marin Islands. *Rattus* occurred on Red Rock in 1934 but the population has now disappeared. Mammals associated with man seem to have been more successful in reaching the islands than native species, despite the much greater span of time available to the latter. It appears that populations of recent mammals were not isolated on the islands when they were formed and that the bay has proven a difficult barrier to their distribution.

Reptiles, because of their more flexible metabolic requirements have a distinct advantage over mammals in survival under conditions of transport as waifs on drifting logs and other debris. This may be significant in their greater success in colonizing the bay islands. The pattern of their occurrence bears little relationship to the favorability of the habitat and this suggests that the populations were established by waiving. The random nature of the reptilian distribution pattern is best illustrated with *Sceloporus occidentalis*. *Sceloporus* is established on East Marin Island although the habitat is not one usually favored and individuals are semi-arboreal in contrast to the ground and rock-dwelling habits of the species on the nearby mainland. Excellent *Sceloporus* habitat is unpopulated on Brooks Island, although the species is common down to the beaches on nearby Pt. Richmond. Such occurrence strongly suggests the influence of chance as a distributional factor.

Amphibians share the metabolic advantages of reptiles but have permeable skins and exposure to sea water is rapidly fatal. On the other hand they tend to inhabit crevices in logs in moist areas where they would be particularly likely to be carried into the bay. Incidence of such castaways is probably high during heavy rain. Since *Batrachoseps* breeds at the start of the rainy season the probability that eggs or gravid females carrying sperm in the spermatheca would be cast adrift would be high. Because *Aneides* breeds after the rainy season the probability of distribution of eggs or gravid females over the bay would be lower than for *Batrachoseps*. In this light the more general distribution of *Batrachoseps* to the islands supports the hypothesis that at least some of the present island populations have been established by waiving. Reference to Table 2 shows that *Batrachoseps*, best suited for waiving by size and breeding habits, has become established on all the bay islands, while *Aneides* shows a random distribution similar to that of the lizards. Further, the *Aneides* populations of Brooks Island and Angel Island are restricted to a very small portion of the available habitat and it seems possible that this signifies that they have only recently become established.

While randomness in distribution pattern is here taken as evidence of waiving, an alternative explanation for random distributions on islands has been

advanced by Darlington (1957). He postulates that random patterns result from extinction on islands which have been isolated after having had mainland connections while regular patterns are produced by waifing, other factors being equal. The latter part of this concept is based on the assumption that waifing, as a random process, would produce a regular and predictable pattern analogous to a normal curve of probability. However, such a pattern would not be produced until the number of waif dispersals was sufficient to meet the statistical requirements for such a curve and an observation in the intervening period would be characterized by randomness of pattern. It appears that such a condition exists in San Francisco Bay.

POTENTIAL FOR WAIF DISTRIBUTION

In view of the distributional evidence for waifing, it seemed worthwhile to conduct an experiment to determine whether or not it was physiologically possible for salamanders to endure the conditions which would be encountered in transport to the islands. *Aneides* and *Batrachoseps* were collected from the beach above the high-tide mark on Red Rock. Animals on this beach may be found on moist gravel beneath objects in the wrack and in association with beach fleas (*Orchestoidea*) and thus might represent the maximum in salinity tolerance. These animals were placed in clean, screw-cap, pint jars. The jar caps were punctured to permit ventilation. To approximate conditions which might be encountered on a drifting log, a folded paper towel was placed in the bottom of the jar together with 50 cc of water of known salinity. The towel surface was above the water level but thoroughly saturated. Animals could rest on the side of the jar, partly or entirely on the moist paper towel, or with part of the body in 2-3 mm of water. The test was conducted in a constant temperature room at 13.5° C.

Salinity in the bay at Red Rock varies from 28 ‰ of dissolved salts (Sept.) to 3 ‰ (maximum runoff periods during rains in Dec.-March) as determined by U. S. Army Engineer Corps studies (unpublished data). Two experiments were conducted to determine the tolerance of salamanders to conditions which would be encountered. In the first, four jars containing 2 adult *Aneides*, 2 adult *Batrachoseps*, 2 adult *Batrachoseps*, and 1 adult *Aneides*, respectively, were provided with water taken from the bay at Red Rock on March 2, 1958. The water sample was taken at the surface 1 hr after high tide. Salinity was 3 ‰ as determined with a hydrometer and salinity tables (USCGS 1952). As a control, animals of similar size were distributed as above in jars containing 50 cc of distilled water. All animals survived in excellent condition throughout a 10-day test period. During the test period the animals were periodically observed and scores were given in accordance with their contact with the water. Higher scores indicated a greater degree of contact. values ranged from 1 for animals on the side of the jar to 6 for animals with most of the ventral

surface in direct contact with the water. Of a possible total of 292 points, the bay-water group scored 138 and the distilled-water group scored 113. It was concluded that water of the salinity found in the bay during periods of high runoff was not avoided by the salamanders and that exposure to surfaces moistened with such water could be tolerated for an indefinite period.

The experiment was repeated with water of 28 ‰ salinity. The same animals were used as in the previous experiment but test and control groups were transposed. After 11 hrs, 5 of the 7 salamanders in the high salinity jars were dead. The remaining two were badly dehydrated, but recovered when placed in fresh water. It appears that transport of salamanders on floating debris is highly improbable outside of the rainy season.

Biological as well as physical agents may be responsible for waif transport. Introduction of salamanders by man is a possibility on all of the islands studied. The probability of its occurrence is highest on Angel Island and Yerba Buena where large numbers of shrubs and trees have been transplanted. High coefficients of variation in the Yerba Buena population may indicate such introduction (Figs. 11-14).

Summarizing the information bearing on the origin of the island populations, amphibians and reptiles of extant species appear to have been present in the bay area since the Pliocene. Populations could have been isolated when the islands were formed at the end of the Pleistocene. Distributional evidence suggests waif dispersal, particularly for *Aneides*, and this is physiologically possible during the rainy season. Universal presence of *Batrachoseps* on the bay islands may be the result of primary isolation in late Pleistocene, waif dispersal, or combination of the two. Human activity may also have influenced distribution. The interval during which the various island populations have been isolated may vary between 10 and 10,000 yrs.

ECOLOGICAL CHARACTERISTICS OF THE SALAMANDER POPULATIONS

DENSITY

It might be expected that the simplification of the island communities discussed above would be reflected in adjustments in population biology. Loss of predatory and competing species could initiate compensations in the population control mechanism and new density levels might result. High density is a frequent phenomenon among island vertebrate populations. While no observations on density of island amphibian populations have been found in the literature, examples of high density among island reptiles are reported by Mertens (1934), Conant & Clay (1937), Camin, Triplehorn & Walter (1954), and Cliff (1954). Changes in density may apparently have direct evolutionary significance. Experimental investigations showing that adaptive values of par-

ticular genotypes differ at high and low densities (Birch 1955, Dobzhansky 1951) support this premise.

Only scattered information is available on the densities of mainland salamander populations. Hendrickson (1954) did not follow his extensive marking program on a *Batrachoseps* population with a capture-recapture analysis of density, but did arrive at an estimate of 1,810 animals/acre by multiplying the number of animals found beneath surface objects in his study area by a factor of 3 to account for those in the surface litter. No density estimates for *Aneides lugubris* have been published. Stebbins (1954) has estimated the density of the slightly smaller sympatric species, *Ensatina eschscholtzi*, in optimum habitat in the Berkeley hills, as about 300/acre in the pre-breeding period of the annual cycle and as 600-700/acre at the time following the emergence of the young. His estimates were based on marking and recapture. Collecting experience gives the impression that densities of *Aneides* in mainland environments are comparable to those of *Ensatina*.

Density of *Aneides* and *Batrachoseps* on the surface is subject to great seasonal variation (Hendrickson 1954, Rosenthal 1957). Despite this, useful impressions of relative density may be obtained in the course of general collecting. With the initiation of field work in the 1956-57 season it was immediately apparent that densities on Red Rock and Brooks Island were much higher than those on the mainland. On Brooks Island the appearance of high density was probably heightened as a result of the burning of the island in October. While lush, new vegetation appeared following the early rains, the layer of duff had been reduced by the fire and the salamanders congregated under the abundant larger covers. In a typical instance 64 *Batrachoseps* were counted under a plank with an area of less than 4 sq ft.

On Red Rock and South Farallon Island a refinement of the technique of general collecting was utilized. On November 4, 1956 a rectangle 20 x 50 ft was marked off on Red Rock in a typical area of favorable habitat and searched intensively for salamanders. This area was on the talus slope where many crevices went down into the earth beyond the level which could be feasibly examined and therefore only animals in the superficial layer could be discovered. In the 1000 sq ft searched 40 *Aneides* and 60 *Batrachoseps* were found. At this time density in the accessible layer was therefore 1250/acre for *Aneides* and 2750/acre for *Batrachoseps*. Actual densities were probably two or three times higher. On South Farallon *Aneides* were scattered over most of the favorable habitat and densities appeared to be 100-200/acre. In two places where concentrations were found areas of 1560 and 840 sq ft were collected intensively and densities of 1030 and 3300 animals/acre were recorded. Such a pattern of scattered animals and local concentrations is typical of mainland popula-

tions and the overall density on South Farallon seemed similar to that on the mainland.

On Brooks Island and Red Rock densities were estimated by marking and recapture in a representative area of favorable habitat. In his study of *Ensatina*, Stebbins (1954) marked animals under covers already present in his study area. The advantage of this technique appears to lie in reduction of disturbance of the area to a minimum. However, some degree of disturbance to the important microclimatic conditions under the extant covers is unavoidable and the advantage may be questionable. An alternate method was chosen for the present study. Covers already present were left undisturbed and small covers of consistent size were placed at regular intervals throughout the area.

The covers added were pieces of well-weathered driftwood gathered on the island beaches or on the bay shore. Planks 2 inch thick were cut into pieces approximately 12 inches square. Some thinner pieces were used and these were weighted with stones. The size was selected with the aim of providing covers large enough to insure suitable humidity and light conditions and attract the salamanders, but small enough to minimize habitat disturbance and attractiveness for potential predators. Preliminary experiments on the University of California campus showed that the size used was adequate to attract salamanders.

Covers were put in place by clearing vegetation from an area equal to that of the cover and pressing the cover firmly against the soil. Covers were placed in a grid at 5-ft intervals. This spacing was designed to place a cover to be used for sampling within the activity radius of every animal present. Hendrickson (1954) estimated the radius of activity for *Batrachoseps* as 5 ft and spacing was based on this estimate since no information was available on the movements of *Aneides* to indicate that a compromise might be necessary to adapt the method to both species.

Procedure in making density estimates on Red Rock and Brooks Island began with marking and release of all animals found beneath the boards. Two weeks later the first effort at recapture was made. In 1957 all animals found on this visit were removed and preserved for later study. The same removal procedure was used on a second visit two weeks after the first. In the density estimates based on the second sample, adjustment was made for marked and unmarked animals removed at the end of the first sampling period by subtracting the animals removed from the values for the number originally marked and for the total population as was appropriate. The removal technique used in the first season permitted collection of comparable samples for study of age structure and reproductive activity and was intended to permit a check on the possibility that new animals might move in to occupy available covers. The number of specimens taken in the second sample was insufficient to carry out the latter analysis reliably. Reduction in sample size suggests that re-

TABLE 4. Movement of *Batrachoseps* in island populations, San Francisco Bay region.

| Area | Period | Rows moved ¹ | No. of individuals | Percent of total recovered | ADJUSTED VALUES ² | |
|---------------|---------|-------------------------|--------------------|----------------------------|------------------------------|---------|
| | | | | | No. | Percent |
| Red Rock..... | Total | 0 | 18 | 82 | 13 | 59 |
| | Study | 1 | 4 | 18 | 9 | 41 |
| Brooks..... | Total | 0 | 42 | 72 | 21 | 26 |
| | Study | 1 | 14 | 24 | 32 | 55 |
| | | 2 | 1 | 2 | 2 | 4 |
| | | 3 | 1 | 2 | 3 | 5 |
| Brooks..... | 14 days | 0 | 35 | 70 | 18 | 36 |
| | | 1 | 14 | 28 | 29 | 58 |
| | | 2 | 0 | 0 | 0 | 0 |
| | | 3 | 1 | 2 | 3 | 6 |
| Brooks..... | 32 days | 0 | 7 | 80 | 4 | 45 |
| | | 1 | 1 | 10 | 2 | 33 |
| | | 2 | 1 | 10 | 3 | 22 |

¹ Each row moved represents a movement of 5 ft. Possible diagonal moves are not considered.

² The adjustment compensates for a limitation inherent in the marking technique which meant that a known fraction of total moves could not be detected (see detailed explanation in text).

placement did not occur but seasonal movements could have obscured a slight influx. In 1958 no animals were removed from the sampling areas.

Data on movement were evaluated in respect to the possibility that the board technique might facilitate the recovery of transients to an extent which would bias density estimates. Movement over distance greater than 10 ft was so rare (Tables 4 and 5) that this possibility was considered to have been eliminated.

Animals were marked by clipping digits with a sharp scalpel while the animal rested on a board.

$$\frac{\text{Number of 5-ft moves recorded}}{\text{Number of 5-ft moves made (X)}}$$

Using the same method, adjusted values may be worked out for 10-ft moves (60 of 140 possibilities can be detected) and for 15-ft moves (40 of 110 possibilities can be detected). Values adjusted by this method differ from the raw data primarily in the higher proportion of 5-ft moves. Diagonal moves, slightly longer than 5 ft, could not be differentiated from horizontal moves between rows. This error would be slight and no corrections were made for it. Movement of *Batrachoseps* recorded in the 1956-57 season is summarized in Table 4. It may be seen from this table that *Batrachoseps* moved frequently during the study period, but that most movements were of only 5 ft and the assumption of a very small activity radius on the islands seems justified.

Since study plots were visited twice following the marking period, the frequency of moves of different length may be compared for shorter and longer periods of time. While the data are too few for reliable interpretation they do not suggest a great difference in frequency or distance of movement between 14-day and 32-day periods.

Movements of *Aneides* on Red Rock are sum-

Batrachoseps were marked by clipping all three large toes from a single limb. *Aneides* were marked by clipping single digits. Little or no trauma appeared to be involved in such mutilation. Many *Batrachoseps* and most *Aneides* would withdraw the limb and move away, but some individuals showed no visible response. When released the animals did not show any evidence of a handicap to movement due to the marking technique. The frequency of occurrence of similar naturally incurred marks was investigated. Of 135 *Batrachoseps*, 2 (1.5%) had mutilations which could have been confused with marks used in the study. Among 222 *Aneides*, 1 (0.5%) had a mutilation which could have been so confused. This natural mutilation would not have influenced the analyses significantly. In the interval of 2-4 wks between marking and recapture there was no possibility of regeneration.

Marked *Batrachoseps* were not individually recognizable but the marks given did permit determination of the row of covers in which an animal had first been captured. In the sample area the covers were divided for marking purposes into 5 rows of 10 boards each. Animals in the first 4 rows were marked on only one foot; right forefoot for the first row, left forefoot for the second row, etc. Those from the 5th row were marked on the left forefoot and the right hind foot. With this system of marking, movement between rows would be detected, but movement from one board to another within the same row would go unrecorded. In the five rows of ten covers there would be 170 possible moves of 5 feet, but only 80 of these would lie between rows and therefore be recorded. This inherent error may be corrected by using the formula:

$$= \frac{80 \text{ (detectable moves)}}{170 \text{ (possible moves)}}$$

marized in Table 5. Since *Aneides* were marked individually no adjustment of figures is necessary. Individual marking also permitted recording of diagonal movements. As with *Batrachoseps* movement over a shorter and longer period may be compared and seems to indicate that stable home ranges exist. It appears that the radius of activity of individuals of both species is about the same on Red Rock and that the 5-ft spacing of sampling covers is therefore appropriate for both species. Individual marking permits a comparison of the movement of adult and subadult animals and the limited data suggest somewhat greater movement by subadults. A similar age-correlated difference was reported for *Ensatina* by Stebbins (1954).

In summary, data on movement serve primarily to support the assumption that the sampling method was valid in respect to surface movements. Neither the data presented here nor the available data on mainland populations suffice for a detailed comparison of movement in island and mainland environments.

Capture/recapture data and resulting density

TABLE 5. Movement of *Aneides* on Red Rock, San Francisco Bay region.

| Period | Distance moved (ft) | No. of individuals | Percent of total recovered |
|-------------|---------------------|--------------------|----------------------------|
| Total Study | 0 | 17 | 57 |
| | 5.0 | 8 | 27 |
| | 7.1 | 3 | 10 |
| | 10.0 | 0 | 0 |
| | 11.4 | 1 | 3 |
| | 15.0 | 1 | 3 |
| 14 days | 0 | 13 | 59 |
| | 5.0 | 6 | 26 |
| | 7.1 | 2 | 10 |
| | 10.0 | 0 | 0 |
| | 11.4 | 1 | 5 |
| 32 days | 0 | 4 | 50 |
| | 5.0 | 2 | 26 |
| | 7.1 | 1 | 12 |
| | 10.1 | 0 | 0 |
| | 11.4 | 0 | 0 |
| | 15.0 | 1 | 12 |

estimates are shown in Table 6. The first estimate of *Batrachoseps* density on Red Rock is based on 84 individuals and can be considered much more reliable than any of the subsequent estimates. Although it is not possible to fully explain the result of the second sampling, an attempt in this direction seems called for. A shift of the population out of the sampling area must have occurred since only a small number of animals were captured. The most promising suggestion seems to be that the summit of the island where the sampling area was located was beginning to dry out as the season progressed and that the animals were moving from beneath surface covers to locations deeper in the soil. It is possibly significant that *Aneides*, which can tolerate more arid conditions, showed no evidence of such a shift. The two 1958 estimates, based on small samples, cannot be considered to be very accurate, but their average value of 6,000/acre approaches the first 1957 estimate. If Hendrickson's estimate of a ratio of 2 animals in surface litter to 1 under larger surface objects is applied to the 1000 sq ft area of intensive collecting referred to previously, the figure of 7,250 *Batrachoseps* per acre lends further support to the first of the mark and recapture estimates. On the basis of this concurrence of somewhat unsatisfactory figures a working estimate of 7,000 *Batrachoseps* per acre of favorable habitat on Red Rock in 1957 appears reasonable.

A more satisfactory agreement was obtained in density estimates on Brooks Island. Again the first 1957 estimate is the most reliable. A density of 4,500 *Batrachoseps* per acre in both 1957 and 1958 is postulated for Brooks Island.

In contrast to the difficulties encountered with *Batrachoseps* estimates on Red Rock, estimates for *Aneides* proved quite consistent. The average of the four capture-recapture estimates (1892/acre) is

TABLE 6. Capture/recapture analysis of salamander populations on Brooks Island and Red Rock, San Francisco Bay.

| Sample | NOM* | NMR | TR | Est. Ind./ft. ² | Ind./acre |
|--------------------------------|------|-----|----|----------------------------|------------|
| <i>Batrachoseps attenuatus</i> | | | | | |
| Red Rock, 17 Feb. 1957 | 103 | 23 | 61 | 0.17 | 7,300 |
| Red Rock, 6 Mar. 1957 | 82 | 1 | 14 | 0.74 | 66,530 |
| Red Rock, 5 Feb. 1958 | 9 | 1 | 11 | 0.09 | 3,870 |
| Red Rock, 2 Mar. 1958 | 9 | 1 | 28 | 0.19 | 8,160 |
| <i>Aneides lugubris</i> | | | | | |
| Brooks, 16 Feb. 1957 | 100 | 49 | 77 | 0.10 | 4,300 |
| Brooks, 2 Mar. 1957 | 51 | 9 | 25 | 0.13 | 5,700 |
| Brooks, 5 Feb. 1958 | 11 | 2 | 19 | 0.09 | 3,870 |
| Brooks, 2 Mar. 1958 | 11 | 3 | 27 | (0.25)** | (10,700)** |
| <i>Aneides lugubris</i> | | | | | |
| Red Rock, 17 Feb. 1957 | 37 | 23 | 39 | 0.038 | 1,640 |
| Red Rock, 6 Mar. 1957 | 14 | 8 | 27 | 0.047 | 2,020 |
| Red Rock, 5 Feb. 1958 | 9 | 3 | 19 | 0.047 | 2,020 |
| Red Rock, 2 Mar. 1958 | 9 | 3 | 18 | 0.044 | 1,890 |

* Abbreviations: NOM—Number of animals originally marked.

NMR—Number of marked animals recovered.

TR—Total animals recovered.

Est. Ind./ft.²—Estimated density in individuals per square foot.

Ind./acre—Estimated density in individuals per acre.

** Figures in parentheses illustrate results which would have been obtained if a single marked animal had been recaptured in addition to the unmarked individuals taken.

rounded off to give a working estimate of 1,900 *Aneides*/acre in favorable habitat on Red Rock.

While these density estimates are not precise they clearly establish the existence of very high densities in the populations of *Batrachoseps* on Brooks Island and Red Rock, and the *Aneides* population on the latter. These densities are in sharp contrast with those of both species on the mainland and with the density of *Aneides* on S. Farallon Island.

POPULATION SIZE

Since Wright (1931 and elsewhere) elucidated the fact that in small populations random processes inherent in the assortment of genetic materials during sexual reproduction can cause non-adaptive loss or fixation of genes there has been considerable interest in the relationship of population size to evolutionary processes. The population involved is not the total number of individuals, but only the number of those effectively contributing to the gene pool of the next generation. With the density data obtained on the islands it is possible to estimate the total number of animals present and then proceed to an estimate of the maximum possible effective population size by investigating population composition. Density data are adequate for this purpose only on Brooks Island and Red Rock.

Population estimates are based on the extent of the favorable habitat (Fig. 1). The north-south line along the crest of Brooks Island sharply divides an area of dense population from one in which *Batrachoseps* are exceedingly scarce. It is felt that this latter area can be eliminated from consideration in estimating the total size of the population. The area of the favorable habitat, as determined by a planimeter reading from an aerial photograph, is 41

acres. At 4,500 animals/acre the *Batrachoseps* population of Brooks Island is estimated as 185,000 animals. Of Red Rock's nine acres, only a small portion is suitable habitat. This area was measured by the same method as above as 2.5 acres. The total *Batrachoseps* population is estimated as 17,500 animals and the total *Aneides* population is estimated as 4,750.

AGE STRUCTURE

No published material is available on age distributions in *Batrachoseps* and *Aneides* populations. On the basis of growth rate and maximum size, Hendrickson (1954) suggested that the life span of *Batrachoseps* in nature may exceed 10 yrs.

The age distribution in a population may be approximated by a frequency distribution of snout-vent length. In the lower range of such a distribution, where growth is rapid, year classes may be clearly distinguished. As the growth rate slows in older animals the differences between age classes are obscured by variations in individual growth rate. The use of such distributions to compare age structure in populations is based upon the following assumptions: First, the shape of the distribution is determined by the same factors determining a true age distribution and by the additional variable of growth rate. Second, a relatively faster or slower growth rate throughout life would shift the distribution as a whole, but would not change its shape. Third, a change in relative growth rates in some age groups, but not in others, could cause a change in the shape of the distribution, but this would not be sufficient to invalidate the comparison.

Annual cycles of breeding activity produce an annually shifting pattern in age structure. This well-known phenomenon requires that samples be taken from comparable points in the annual cycle of the populations to be compared. Mainland samples of *Batrachoseps* from which snout-vent distributions were drawn were taken between December 24th and February 10th. This interval precedes the appearance of most newly hatched animals on the surface and it is at this time that the proportion of older individuals would be highest. Island samples shown were collected between November 4th and March 6th. The bias introduced by the inclusion of the island samples from late February and March would be in the direction of reduced proportions of adult individuals following the appearance of young of the year. Because reproductive activity on the islands was limited, this bias is slight and it was felt that the disadvantage incurred by ignoring it was outweighed by the advantage of using the largest possible samples. The adequacy of the sample size available may be evaluated by comparing pairs of samples from the same or nearby populations collected within a short interval of time. Comparison of such pairs for *Batrachoseps* and *Aneides* populations (Figs. 4 and 5) shows consistency in overall shape but not in exact detail. This consistency is

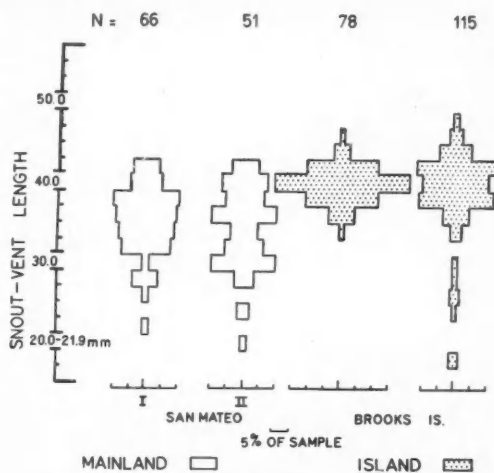


Fig. 4. Pairs of snout-vent frequency histograms illustrating consistency in samples of *Batrachoseps* populations. The two San Mateo collections were made on Feb. 10, 1957, about 5 mi apart. The two Brooks Island samples were taken on Dec. 15, 1956 (N=115) and on Feb. 16, 1957 (N=78). Percent of sample in each size group is indicated by horizontal extent of histogram.

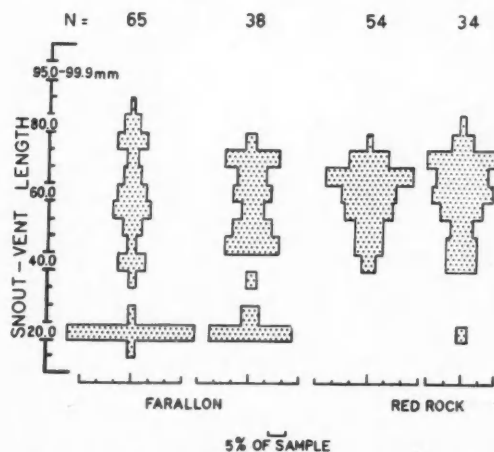


Fig. 5. Pairs of snout-vent frequency histograms illustrating consistency in *Aneides* samples. Farallon samples were taken December 20-23, 1956, Red Rock samples were taken on February 17, 1957 (N=34) and November 4, 1956.

adequate for evaluation of the general structural characteristics of the populations.

In Fig. 6 age structure as represented by snout-vent frequency distributions in island and mainland *Batrachoseps* is shown. There appears to be a clear cut difference between the pattern on the smaller islands on the one hand and that of Angel Island and the mainland on the other. The small island distributions are compressed, with almost all individuals falling into the larger size groups. Such a pre-

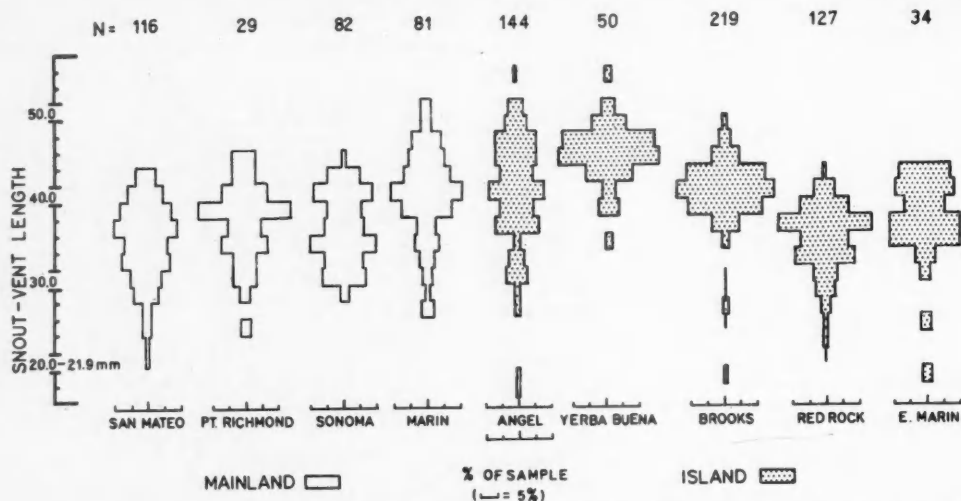


Fig. 6. Comparison of age structure as represented by snout-vent frequency histograms in island and mainland populations of *Batrachoseps*, San Francisco Bay region.

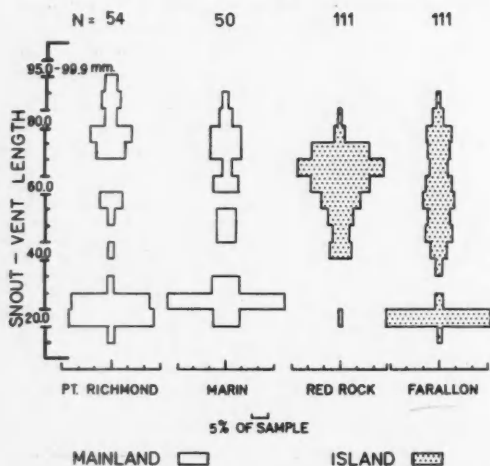


Fig. 7. Comparison of age structure as represented by snout-vent frequency histograms in island and mainland populations of *Aneides*, San Francisco Bay region.

dominance of older animals implies both low mortality of adults and a sharp reduction in realized reproductive output for one and possibly two previous seasons.

In Fig. 7 comparison of the Red Rock population of *Aneides* with those on the mainland and on South Farallon Island shows a similar situation. The samples were taken during the phase of the reproductive cycle following the appearance of newly hatched young and this is reflected in the shape of mainland and South Farallon distributions. A comparative lack of reproductive activity for at least two years previously is indicated by the Red Rock distribution. The close proximity of Red Rock and Brooks Is-

land to Pt. Richmond rules out the possibility of climatic factors as a cause of these differences in age distribution and the similarity of Farallon and mainland *Aneides* populations despite greater climatic differences also argues against such an explanation. Higher mortality of the young in an island environment seems unlikely and a shift in reproductive activity, associated with high density, seemed a probable cause of the age structure observed. The existence of such a shift, and some of the mechanisms involved, were established by an investigation of reproductive activity in island and mainland populations.

REPRODUCTIVE STRUCTURE

Despite the ease with which the statistics are obtained there seem to be no published data on sex ratios in *Aneides* or *Batrachoseps* populations. Sex ratios for other plethodontid salamanders have been published by Blanchard (1935) who reported 0.76 ♂/♀ in *Hemidactylium scutatum* and by Gordon (1953) who found the sexes equal in number in *Eurycea longicauda guttolineata*. Sex ratios in collections of amphibians may vary with the collecting technique and with the season. Examples of such variation in *Batrachoseps* and *Aneides* may be seen in Table 7. The Berkeley sample, collected on October 26, 1956, was obtained along a dirt road in Strawberry Canyon during a heavy rain and appeared to be biased by breeding activity. Almost all animals found were gravid females and were moving in the same direction (up hill and across the road). In order to cross the road and the shoulders on either side a minimum movement of 30 ft across uninhabitable terrain was required. Such long distance movement indicates special circumstances and supports the hypothesis that the sample was biased by breeding activity.

TABLE 7. Sex ratios in population samples of *Batrachoseps* and *Aneides*, San Francisco Bay region. Adult and subadult individuals included.

| Locality | Date | BATRACHOSEPS | | ANEIDES | |
|-----------------------|----------------|--------------|------|---------|------|
| | | N | ♂♂/♀ | N | ♂♂/♀ |
| Mainland: | | | | | |
| San Mateo I..... | 10 Feb. '57 | 51 | 0.89 | | |
| San Mateo II..... | 10 Feb. '57 | 66 | 0.94 | | |
| Berkeley..... | 26 Oct. '56 | 69 | 0.17 | | |
| | 8 Apr. '57 | 16 | 1.67 | | |
| Pt. Richmond..... | 8 Feb. '57 | 29 | 0.71 | 26 | 0.73 |
| Sonoma..... | 9 Feb. '57 | 82 | 1.05 | | |
| Marin I..... | 24 Dec. '57 | 55 | 0.77 | | |
| Marin II..... | 24 Dec. '57 | 26 | 0.73 | | |
| Marin (combined)..... | 24 Dec. '57 | ... | | 26 | 0.75 |
| Island: | | | | | |
| Angel..... | 10 Nov. '56 | 30 | 2.00 | | |
| | 16 Dec. '56 | 37 | 0.60 | | |
| | 9 Feb. '58 | 77 | 4.50 | | |
| Yerba Buena..... | 1 Mar. '57 | 50 | 1.78 | | |
| Brooks Is..... | 15 Dec. '56 | 115 | 1.45 | | |
| | 16 Feb. '57 | 78 | 1.05 | | |
| | 2 Mar. '57 | 26 | 1.17 | | |
| Red Rock..... | 4 Nov. '56 | 65 | 0.76 | 50 | 0.92 |
| | 17 Feb. '57 | 48 | 1.18 | | |
| | 6 Mar. '57 | ... | | 27 | 0.93 |
| S. Farallon..... | 20-23 Dec. '56 | ... | | 72 | 1.00 |

A second strongly skewed sex ratio was recorded from Angel Island on February 9, 1958. There is no apparent explanation for the high proportion of males represented in this sample.

Despite the complications referred to above, Table 7 as a whole shows a trend toward a higher proportion of males in the island populations. Selecting *Batrachoseps* samples collected under the same circumstances at the same time of year (February 8 to March 1) we may test the apparent difference for statistical significance. The ratio of males to females in the pooled San Mateo, Point Richmond, and Sonoma samples is 0.93 ♂♂/♀. Pooled island samples taken from Yerba Buena, Brooks Island and Red Rock during this period have a ratio of 1.25 ♂♂/♀. The sizes of the pooled samples are 228 and 202 animals respectively. Comparison of the two by the chi-squared method (Mayr, Linsley & Usinger 1953) gives a value of 2.246, indicating that the difference is not significant at the 95% level of confidence. A similar trend in sex ratio is shown in *Aneides* samples, but sample size is too small for meaningful analysis.

In the introductory review of the biology of *Batrachoseps* it was noted that gravid females may be found beneath surface objects during the first two weeks of surface activity which follow the beginning of the rainy season. By the end of this 2-wk period almost all mainland females have de-

posited their eggs. In the fall of 1956, Red Rock was visited during this interval and 65 animals, of which 30 were adult females, were collected. None was gravid. No gravid females were found in subsequent visits. On Brooks Island, a contrasting situation was found. The first sample there was taken one month later, when gravid females had become very rare on the mainland. Gravid females were common in this Brooks Island sample and they remained so for four months. The proportions of females which were gravid in collections from Brooks Island were as follows: December 15, 1957, 15% of 46 females gravid; February 17, 1957, 13% of 38 females gravid; and March 2, 1957, 42% of 12 females gravid. Mature ovarian oocytes of 3 of the 5 gravid females found on March 2nd showed signs of deterioration (= resorption?) when the preserved specimens were examined. This apparent reproductive inhibition in the island populations was re-emphasized by observations later in the season when newly hatched young had made their appearance on the mainland. No such young were found on Red Rock and relatively few were found on Brooks Island. Field observation indicated, therefore, that most or all adult female *Batrachoseps* on Red Rock failed to develop mature oocytes, while many adult females on Brooks Island developed large oocytes but did not oviposit and eventually resorbed their eggs. Observations in the fall and spring of the 1957-58 season indicated that these conditions changed to some degree. The extent of breeding activity was not determined, but a single gravid female was found among 8 individuals taken on Red Rock on October 15th, and newly hatched young were found on February 5th and March 2nd. On Brooks Island no gravid females were found among 10 unsexed individuals examined in the field on February 5th, nor among 27 examined on March 2nd.

Since *Aneides* eggs are deposited in late spring or early summer, recently hatched young would be expected in fall and winter collections. Such animals are included in the 15-30 mm size group in Fig. 7. The disparity between Red Rock and Point Richmond may be illustrated by comparison of a sample from the latter locality taken on February 8, 1957, which contained 28 hatchlings out of a total of 54 individuals, with a sample of 38 individuals taken on Red Rock on Feb. 17, 1957 which contained no hatchlings. As was the case with *Batrachoseps*, this situation had changed to some extent in 1957-58. One of 18 individuals taken on Red Rock on March 2, 1958 was a hatchling. The evidence of low natality over the previous two year period suggested by the age distributions for Red Rock and Brooks Island salamanders is therefore supported and extended through the 1956-57 season by field observations.

To elucidate further the relative reproductive status of the island and mainland populations, samples were preserved for dissection in the laboratory. Gonads were examined under a dissecting microscope, measured, and placed in categories by comparison

TABLE 8. Categories for classification of *Batrachoseps* gonads.

| Category | Description | Status |
|-----------------|--|----------------------------|
| Ovaries: | | |
| A | Oocytes small, clear or opaque, with no distinct size classes. | juvenile |
| B | Oocytes in two or more size classes but none with sufficient yolk to give a yellow color. Individuals which will probably breed for the first time in the next season, or inactive adults. A few post-ovulatory females may be included in this class. | subadult or inactive adult |
| C | Large oocytes (1.0 mm. in dia.) present and and yellow with stored yolk. Includes class D, as well as most post-ovulatory individuals. ¹ | adult |
| D | Gravid class C females. Oocytes have a diameter of 3.0 mm. | pre-ovulatory adult |
| Testes: | | |
| A | Small, unswollen, unpigmented. | juvenile |
| B | Large, but unswollen and with little or no pigment. | subadult or inactive adult |
| C | Large, swollen, gonad and duct often heavily pigmented. | active adult |

¹ Appearance of post-ovulatory gonads was established by examination of 22 females which had been induced to ovulate in the laboratory.

with a series of preserved gonads selected to represent all stages of reproductive activity found in the populations investigated. The sample gonads were placed in glass tubes so that they could be compared directly with those of animals being examined under a dissecting microscope. Categories used and their interpretation are described in Table 8 and 9.

In Table 10 the frequency of the various reproductive categories in population samples of female *Batrachoseps* collected between February 9th and 17th, 1957 is shown. Mainland samples show a reasonably consistent pattern in which an average of 22% of all females are reproductively active. On Brooks Island two striking shifts have taken place: the majority of reproductively active females have retained their eggs (the 16% in Class "D"), leaving only 8% which had presumably ovulated and oviposited in the last breeding season, and a marked increase has taken place in the number of females in the sub-adult category. Reference to the snout-vent length distribution (Fig. 6) makes this latter shift even more striking since all females in the population are above 34.0 mm in snout-vent length. This is the smallest size recorded among 59 gravid females collected at Berkeley in the previous October and is taken as minimum adult size. It appears, therefore, that on Brooks Island female reproductive activity was being reduced in two ways, by inhibition of gonadal development ("subadult" and "juvenile" ovaries in full grown individuals), and by inhibition of oviposition (retention of mature oocytes and their eventual resorption).

On Red Rock a different pattern is disclosed. Here no definitely active females were found and a

TABLE 9. Categories for classification of *Aneides* gonads.

| Category | Description | Status |
|-----------------|---|----------------------------------|
| Ovaries: | | |
| A | Oocytes small, clear or opaque, with no distinct size classes. | juvenile |
| B | Oocytes in two size classes, larger about 0.6 mm. in diameter, probably will not reproduce this year. | subadult |
| C | Largest oocytes about 1.5 mm. in diameter. May be animals which will reproduce for the first time in the coming season or inactive adults. | young adult or inactive adult(?) |
| D | Largest oocytes 3.0 mm. in diameter, yellow with yolk. Active individuals ready for coming breeding season. | adult |
| E | Evidence of past reproductive activity (yellow yolk-like deposits which may indicate atresia). Large adults without large oocytes in the ovaries. | inactive adult |
| Testes: | | |
| A | Small, unpigmented | juvenile |
| B | Intermediate in size, little or no pigment. | subadult or inactive adult |
| C | Gonad and vas deferens large, swollen, partially or heavily pigmented. | adult |
| D | Gonad and vas deferens heavily pigmented but shriveled in appearance. Animal large, often emaciated. | inactive adult |

TABLE 10. Reproductive categories in *Batrachoseps* samples, San Francisco Bay region.¹

| Reprod. Category | San Mateo I | San Mateo II | Sonoma | Mainland av. | Brooks Island | Red Rock |
|------------------|-------------|--------------|----------|--------------|----------------------|----------|
| Females | N=28 | N=33 | N=40 | | N=38 | N=22 |
| A..... | 50% (14) | 24% (8) | 37% (15) | 37% | 5% (2) | 68% (15) |
| B..... | 29% (8) | 49% (16) | 45% (18) | 41% | 71% (27) | 32% (7) |
| C..... | 21% (6) | 27% (9) | 18% (7) | 22% | 24% (9) | 0 |
| D..... | 0 | 0 | 0 | 0 | 16% (6) ² | 0 |
| Males | N=23 | N=33 | N=33 | | N=39 | N=28 |
| A..... | 4% (1) | 0 | 6% (2) | 3% | 10% (4) | 0 |
| B..... | 66% (15) | 55% (18) | 88% (29) | 70% | 90% (35) | 89% (25) |
| C..... | 30% (7) | 45% (15) | 6% (2) | 27% | 0 | 11% (3) |

¹ Refer to Table 8 for clarification of categories.

² Category D is combined with category C.

very high proportion of the ovaries (68%) appeared to be fully juvenile, despite the fact that three-fourths of the animals were of adult size (Fig. 7). Inhibition of gonadal development seemed to have been extreme and may have involved the whole population of adult females.

The frequency of the various reproductive categories in male *Batrachoseps* in the same samples is also shown in Table 10. Island populations fall close to the extreme of mainland variation as represented by the Sonoma sample, but the small proportion of definitely adult males is at least suggestive of inhibition of male reproductive activity paralleling that of the females.

TABLE 11. Reproductive categories in *Aneides* samples, San Francisco Bay region.¹

| | Mainland ² 26 Dec.-8 Feb. | Farallon 20-23 Dec. | Red Rock ³ 17 Feb.-7 Mar. |
|----------------|---|------------------------|---|
| Females..... | N=59 | N=50 | N=30 |
| hatchling..... | 37% (22) | 28% (14) | 2% (0.5) ⁴ |
| A..... | 22% (13) | 36% (18) | 20% (6) |
| B..... | 10% (6) | 0 | 7% (2) |
| C..... | 7% (4) | 8% (4) | 43% (13) |
| D..... | 24% (14) | 22% (11) | 16% (5) |
| E..... | 0 | 6% (3) | 13% (4) |
| Males | | | |
| hatchling..... | 44% (22) | 28% (14) | 2% (0.5) ⁴ |
| A..... | 12% (6) | 43% (21) | 24% (7) |
| B..... | 10% (5) | 4% (2) | 14% (4) |
| C..... | 34% (17) | 22% (11) | 23% (6) |
| D..... | 0 | 2% (1) | 38% (11) |

¹ Refer to table 9 for clarification of categories.² Pooled samples from Marin County and Pt. Richmond.³ Red Rock proportions were similar in a sample collected on Nov. 4. Any bias introduced by the later dates of the Red Rock sample would produce a trend opposite from that observed.⁴ One hatchling only found. Specimen could not be sexed on gross examination.

In Table 11 the frequency of reproductive categories in female *Aneides* collected between December 20, 1956 and February 17, 1957 is presented. A 50/50 sex ratio has been assumed for the hatchlings since it was not possible to sex them by gross examination. Reference to the table shows that reproductive activity in mainland and Farallon populations is similar, with the exceptions that no subadult females were found in the Farallon sample while a small proportion of individuals with inactive (Category E) ovaries occurred. On Red Rock this inactive portion, and that of dubiously active adults (Category C), become substantially larger, while the proportion of active adults is reduced. The extent of this difference is masked by the relative scarcity of hatchlings on Red Rock, and if only mature animals are compared 55% and 60% of mainland and Farallon adults, respectively, are in Class D as compared to 24% of Red Rock adults in the same active condition.

The most prominent feature of Table 11 concerning the frequency of reproductive categories in male *Aneides* is the predominance on Red Rock of males with apparently regressed gonads. The appearance of such gonads is strikingly different from those in a normal state of activity and, although no histological examination was made, the assumption seems justified that the shriveled and shrunken appearance of both gonads and ducts indicates a lack of sexual activity.

EFFECTIVE BREEDING POPULATIONS

The data on the reproductive activity which have just been discussed permit estimation of maximum possible effective population size. Since different levels (and mechanisms) of reproductive inhibition appear to be involved in the different populations, it is instructive to see what the effect of each would be if it were in operation in a given population. Table 12 illustrates the maximum possible effective breeding populations which would result on the is-

TABLE 12. Potential reduction in effective breeding populations of *Batrachoseps* and *Aneides* through shifts in reproductive structure.

| Reproductive structure equivalent to: | Percent of population active | Maximum breeding population | |
|---------------------------------------|------------------------------|-----------------------------------|--|
| <i>Batrachoseps</i> | | <i>Brooks Island</i> (185,000) | <i>Red Rock</i> (17,500) ¹ |
| Mainland..... | 22% | 41,000 | 3,500 |
| Brooks Island..... | 8% | 14,800 ² | 1,400 |
| Red Rock..... | 1% or less | 1,850 | 175 |
| <i>Aneides</i> | | | (4,750) |
| Mainland..... | 24% | — | 1,140 |
| Red Rock..... | 16% | — | 760 |

¹ Estimates of total populations are shown in parentheses.² Estimates underlined indicate maximum size of the populations actually effective.

lands if reproductive structure conformed to the various patterns noted above. The calculations are based on reproductive activity among females on the assumption that one male may transmit spermatophores to several females, but that the latter mate only once, and that reproductive activity among females is the more important limiting factor in determining the number of individuals capable of contributing to the future gene pool. It should be kept in mind that data are not available on the duration of the reproductive inhibition and that given females might be inactive only in alternate years. The table, therefore, can only indicate the potential effects of the phenomena observed and set an upper limit to the actual effective breeding size, which is influenced by individual movement and other factors and remains unknown. Even if inhibition is only periodic, coinciding with the highs of a fluctuating population (during which the breeding population, paradoxically, would be lowered), the phenomenon appears capable of increasing the chance for genetic drift. This assumption is based on Wright's (1939) demonstration that the effective population size is the harmonic mean of a fluctuating population and lies nearest the minimum value.

REGULATION OF NUMBERS

The readjustment of reproductive structure described for the salamander populations of Red Rock and Brooks Island is associated with the high densities observed and did not occur on South Farallon where density appeared to be low. There are indications in the literature that crowding may induce reproductive inhibition in vertebrates. Regression of ovaries to a juvenile condition in correlation with high density has been reported in experimental populations of the frog, *Xenopus laevis* by Alexander & Bellerby (1938), and the house mouse, *Mus musculus* by Crowcroft & Rowe (1957). It is possible, therefore, that the adjustments observed on Brooks Island and Red Rock represent reactions to high density. The age structure of these populations implies that mortality and emigration must play a reduced role in control of density and that control mechanisms

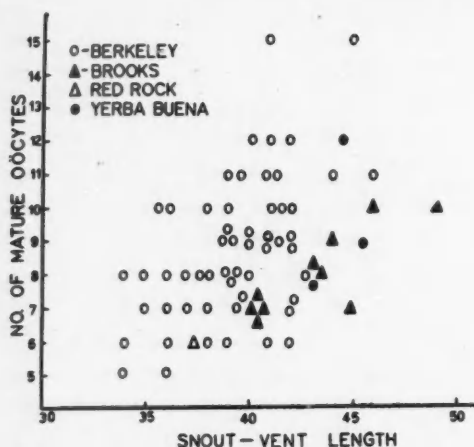


Fig. 8. Clutch size in *Batrachoseps* as determined by counts of mature ovarian oocytes of island and mainland individuals.

operating at the natality level have been forced to assume a greater responsibility.

In addition to shifts in reproductive structure, control at the natality level through adjustment of clutch size might be expected. Clutch size for island and mainland populations of *Batrachoseps*, as determined by counts of mature ova in gravid females, is shown in Fig. 8. Mean clutch size for Brooks Island animals was 8.0 as contrasted to 8.7 on the mainland, despite the larger average size of Brooks Island females. Expressed as ova per millimeter of snout-vent length the average value for mainland animals is 0.223 as opposed to 0.186 for those from Brooks Island. The difference between these means is significant beyond the 95% level as evaluated by the "t" test (Dixon & Massey 1951).

Some simple calculations show that these intra-specific mechanisms can be very effective in limiting reproductive output. Using the local reproductive structure as indicated in Table 11 and the mean clutch size of Brooks Island females for both island populations, I estimated the annual egg production per cohort of 1000 females of all ages as 1914 eggs on the mainland, 640 on Brooks Island, and 80 or fewer on Red Rock.

In *Aneides*, counts of oocytes in the largest (3.0 mm) size class in the ovaries of females in the "D" category were used as an index of clutch size. Reduction in clutch size was found in island populations (Fig. 9). The pattern of this reduction differs from that in *Batrachoseps* in that island and mainland populations lie along the same regression line and the difference in fecundity is associated with the smaller size of sexually active females. Annual fecundity per 1000 females may be calculated as 4,992 on the mainland, 2,552 on South Farallon, and 1,760 on Red Rock, based on the percentage of individuals in category "D" (Table 11) and on mean clutch sizes of 20.8, 11.6, and 11.0 respectively. While

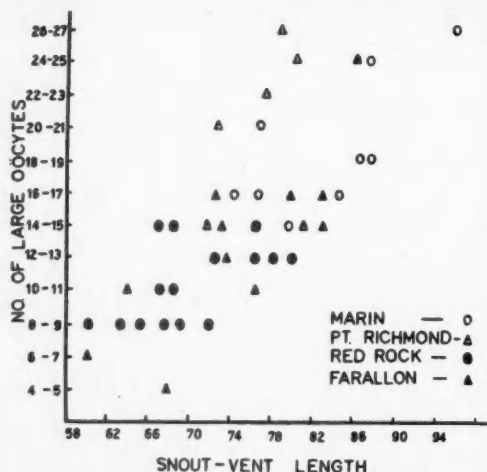


Fig. 9. Clutch size in *Aneides* as determined by counts of maturing ovarian oocytes of island and mainland individuals.

no pretense is made that these data are accurate in detail, the estimates demonstrate the potential effectiveness of the observed changes in reproductive structure and in clutch size as population control factors. Since survivorship appears to be high on the islands and emigration nil, it would appear that reduced natality has been brought into play in lowering the rate of increase.

If the reproductive inhibition observed on Brooks Island and on Red Rock were inflexibly maintained the populations would soon become extinct. It may be postulated, therefore, that high population density and the resulting reproductive inhibition interact to cause cycles in which high density and reproductive inhibition alternate with periods of lowered density and increased reproductive output. Such cyclic phenomena on the islands would be the result of reliance on the internal control mechanisms which apparently was forced upon the population by the absence or effective reduction of such external controls as predation.

SUMMARY OF ECOLOGICAL VARIATION

The island habitats of *Batrachoseps* and *Aneides* include few ecological associations and, in general, fewer species per association than is the case on the nearby mainland. The result is a simplification of the matrix of ecological factors in which the population functions. Specifically, decreases in the number of prey species in the diet, and in the number of kinds of predators, show that such simplification bears on the biology of the salamander populations investigated.

Analysis of age structure shows that the salamander populations of the smaller islands in the Bay are characterized by a relatively large number of older animals. On Red Rock and Brooks Island, where intensive studies were carried out, this shift in

age structure was associated with very high densities. Density appeared to be low on South Farallon Island and no shift in age structure was found.

The observed shift in age structure implied low adult mortality and reduced reproductive output. Investigation of reproductive activity in the dense populations showed reproductive inhibition of two types in females, some evidence of inhibition in males, and reduction in the clutch size of those females reproducing. On South Farallon, only a change in clutch size was found. The coincidence of high density and reproductive inhibition on Brooks Island and Red Rock suggest that population control factors have changed in the island environments and that intraspecific factors, operating to lower natality, have been emphasized. The potential effectiveness of these factors in lowering both the breeding population and the annual reproductive output suggests that they are significant control mechanisms.

MORPHOLOGICAL CHARACTERISTICS OF THE POPULATIONS

Analysis of the ecological conditions and of the dynamics of the island salamander populations was made with the hope of discovering how they might contribute to the development of genetic divergence. The population characteristics themselves were assumed to be based on inheritable attributes of individuals, but this cannot be specifically demonstrated in the present case and the phenotypic flexibility of the individuals, as well as the resulting flexibility of the populations, is unknown. Analysis of the degree to which the island populations have evolved divergent attributes could best be carried out by means of standard systematic techniques, using characteristics for which a genetic basis is generally accepted. The objectives were to determine the extent of divergence, if any; to consider the zoogeographic and evolutionary significance of any pattern disclosed; and to ascertain if a change in the extent of morphological variability is characteristic of island populations as compared with those of the mainland. Finally, the patterns of morphological variation were reviewed in search of correlations with certain gross aspects of specific islands, such as their size and relative degree of isolation.

METHODS

Animals were anesthetized with chlorotone or tricane methane sulfonate before hardening in 5% formalin. This permitted arrangement of the specimens in positions favorable for subsequent measurement. Final preservation was in 65% alcohol. Measurements were taken with a vernier caliper or with an ocular micrometer in a Spencer dissecting microscope at 9X magnification as appropriate to the specimen and the measurement concerned. Morphological characteristics utilized were defined as follows: Snout-vent length—the distance from the tip of the snout to the rear of the vent; tail length—the distance from the rear of the vent to the tip of

the tail; head width—a straight line between the corners of the mouth; limb length—measured on the forelimb as the distance from the body to the elbow along the dorsal surface of the limb with the humerus horizontal and the forearm vertical; number of yellow spots (*Aneides*)—counted on the 4th through 7th costal folds behind the axilla on the left side between mid-dorsal line and ventral limit of dorsal pigmentation; diameter of yellow spots (*Aneides*)—taken as the average diameter of the first 5 spots counted behind the anterior margin of the 4th costal fold (if less than 5 were present on folds 4-7, the average diameter of those present was taken); vomerine teeth—total on both sides as counted with the aid of the dissecting microscope and a small air jet; palatine teeth (*Aneides*)—total in right or left patch counted with the aid of the dissecting microscope and air jet; costal grooves—counted as including all grooves entering axilla and groin. Samples studied were taken at the mainland and island localities indicated in Fig. 1 and on South Farallon Island.

The analysis of variation was undertaken for the light it might shed on evolutionary mechanisms, rather than on systematic interpretation. The data presented are of possible systematic significance, but I believe that this can be evaluated only in the course of a review of variation over a much greater area than is covered in this study. Systematic questions are therefore not considered here.

VARIATION IN BATRACHOSEPS

Variation in *Batrachoseps* populations is shown in Figs. 10-14. In these figures the samples are arranged with reference to their geographic locations so that, reading from the top downward, the localities lie in a clockwise arc around the bay. This permits the ready comparison of contiguous samples. To reduce the possibility of distortion due to ontogenetic variation Figs. 11-14 are based on specimens 30.0 mm or greater in snout-vent length.

Referring to the figures, it may be seen that mainland populations on the Marin Peninsula, at Sonoma, and at the far extreme of the arc in San Mateo County, approximate each other closely in all respects. These populations are taken as representative of a "mainland" type, and this is indicated by the shaded area showing the range of their standard deviations in four of the figures. The Berkeley and Point Richmond populations diverge from this pattern and the extreme is reached in all cases at Point Richmond. Berkeley is intermediate between Point Richmond and the other mainland localities in three characteristics.

There is no indication of an "island" type in contrast to that of the mainland. Among the island populations, those on Brooks and Red Rock show striking divergence from the mainland type and even greater divergence from each other. Moreover, the Brooks Island population has its closest affinities with the Point Richmond and Berkeley populations while that on Red Rock is closest to the general main-

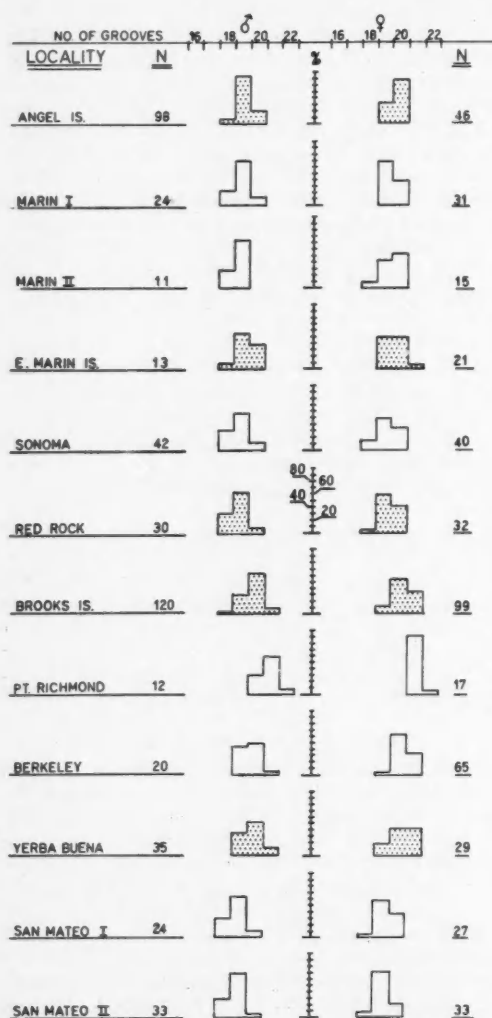


Fig. 10. Variation in costal groove counts in *Batrachoseps* populations. Sexes are dimorphic and are compared separately. Histograms show frequency in percent in samples whose sizes are indicated under "N."

land type despite its geographical location near the Point Richmond land mass. Angel Island and East Marin Island populations show affinities to that of Red Rock, especially in body proportions. Angel Island animals show divergent tendencies with respect to the mainland in vomerine tooth count. Yerba Buena generally falls within or close to the mainland type. The data establish the occurrence of statistically significant morphological variation between each island and the neighboring mainland in at least one characteristic in every case. The smaller islands, East Marin and Red Rock, tend to diverge more from the nearest mainland population than do the larger islands.

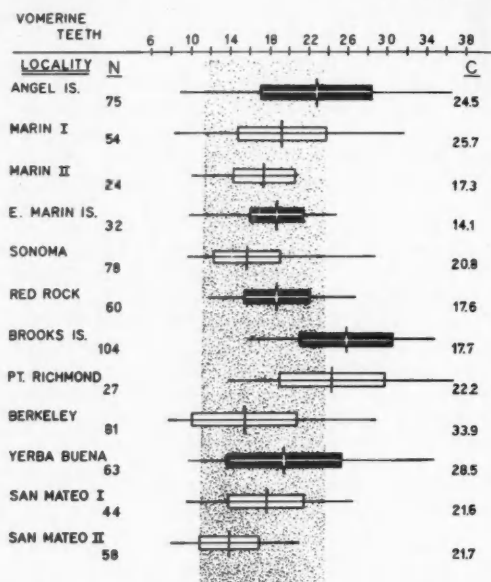


Fig. 11. Variation in vomerine tooth counts in *Batrachoseps* populations. Rectangle indicates one standard deviation on either side of the mean. Shaded area indicates range of standard deviations of populations taken as belonging to the "mainland type." Sample size is indicated to the left, coefficients of variation to the right of each sample.

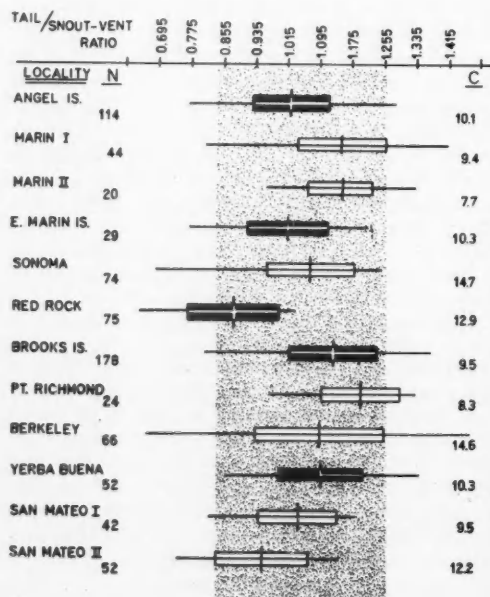


Fig. 12. Variation in the ratio of tail length to snout-vent length in *Batrachoseps* populations. See Fig. 12 for clarification of presentation.

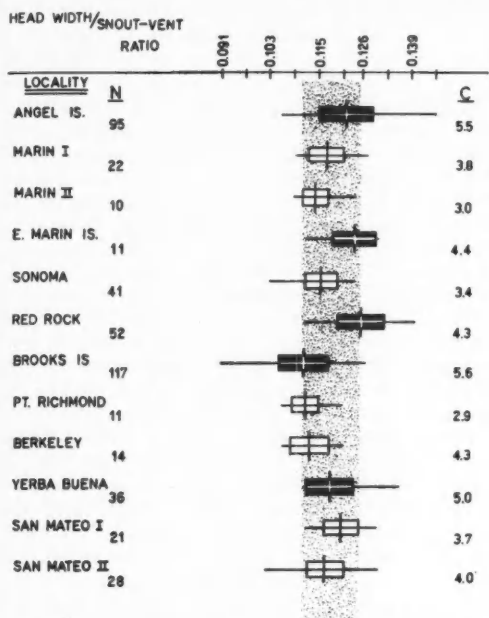


Fig. 13. Variation in the ratio of head width to snout-vent length in *Batrachoseps* populations. See Fig. 12 for clarification of presentation.

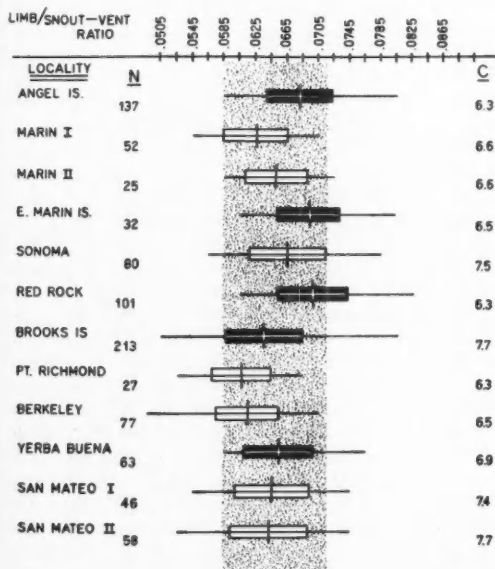


Fig. 14. Variation in the ratio of limb length to snout-vent length in *Batrachoseps* populations. See Fig. 12 for clarification of presentation.

Internal variability of each population studied is expressed in Fig. 11-14 as standard deviation and as a coefficient of variation. The coefficients are not significantly smaller on the islands as a group in

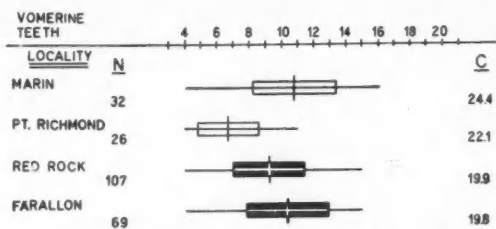


Fig. 15. Variation in vomerine teeth in *Aneides* populations. See Fig. 12 for clarification of presentation.

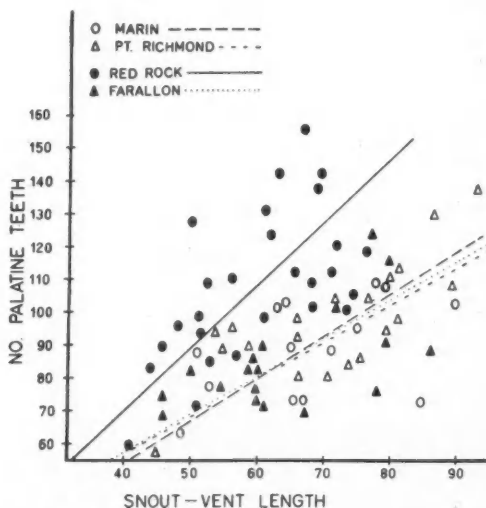


Fig. 16. Variation in the number of palatine teeth in *Aneides* populations. Teeth counted in either right or left patch, regression lines drawn by inspection.

comparison with the mainland populations. Berkeley and Point Richmond populations tend to have high coefficients, as does that on Yerba Buena. In comparison with mainland localities other than Berkeley and Point Richmond the populations of the smaller islands, Red Rock and East Marin, show low coefficients in 2 and 3 of the 4 characteristics, respectively. These differences are slight and a conclusion that variability is restricted on the islands does not seem justified.

VARIATION IN *Aneides*

Variation in *Aneides* was investigated on the basis of a pooled sample from the two Marin peninsula localities and samples from Point Richmond, Red Rock and South Farallon Island. The characters studied were: number of vomerine and palatine teeth, number of yellow spots, and size of yellow spots (Figs. 15-18). To avoid bias due to ontogenetic variation only individuals over 40.0 mm in snout-vent length are included. Coastal groove counts were not used since they show almost no variation among the *Aneides* populations of the area.

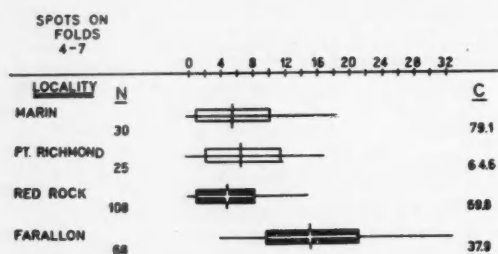


Fig. 17. Variation in the number of yellow spots in *Aneides* populations. Spots counted on folds four through seven on the left side. Presentation as in Fig. 12.

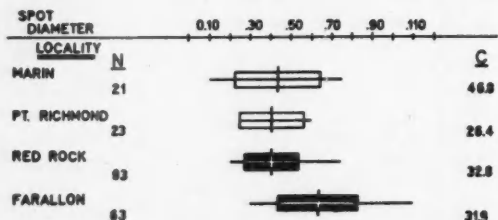


Fig. 18. Variation in the diameter of yellow spots in *Aneides* populations. Average values in mm. of five or fewer spots occurring on coastal folds on the left side. Presentation as in Fig. 12.

The Red Rock population appears to be identical with the two mainland samples in color pattern and falls between the divergent Point Richmond and Marin samples in vomerine tooth counts. It is clearly divergent from all other populations in the high number of palatine teeth. Unlike the Red Rock *Batrachoseps* population it does not show stronger affinities to the Marin population than to Point Richmond and it diverges from both in approximately equal degree in palatine tooth counts. The lack of consistent divergence between Point Richmond and Red Rock in the *Aneides* populations is noteworthy in comparison with the situation in *Batrachoseps*, since it may indicate that the *Aneides* population has been more recently established.

The Farallon population is divergent only in color pattern characters. The coloration is quite similar to that of animals from the southern side of the Salinas valley but this area is over 100 sea miles distant so that the probability of arrival of waifs in drifting logs from that source is very low. Human transport or convergence seem to be the possible alternative explanations for this similarity and the question could probably be settled by a careful comparison of the two populations. Too many unknowns are involved to permit speculation as to whether Red Rock *Aneides* have undergone more, or less, divergence than those on the larger, but more isolated, Farallon Island, the fact that the latter population is considered a subspecies notwithstanding.

Coefficients of variation are shown in Figs. 15, 17, and 18, but do not appear to indicate any signif-

icant difference in intra-population variability between island and mainland samples.

DISCUSSION

The foregoing study of morphological variation has shown that each island population has diverged from the adjacent mainland at a statistically significant level in at least one of the characters studied. Levels of divergence usually considered taxonomically significant are reached between the Red Rock and Pt. Richmond populations of *Batrachoseps*, between Red Rock and Pt. Richmond populations of *Aneides*, and between Farallon and Marin populations of *Aneides*. Variation among mainland populations is sufficient to cause some overlap in standard deviations for each character studied between each island population and a mainland locality other than that nearest the island. The only possible exception to this is the palatine tooth character in Red Rock *Aneides*. Such overlap may be the result of common ancestry, adaptive convergence, random drift in the island populations, or gene flow from the mainland area to the island. The interpretation of these patterns of divergence and convergence with respect to the historical and ecological background delineated in this study will be initiated by considering the way in which the manner of origin of an island population can influence its subsequent divergence.

The patterns of distribution and variation of amphibians about San Francisco Bay, as compared with those of birds and mammals, suggest that the amphibian species are both more conservative and more ancient. The evidence indicates that *Batrachoseps* and *Aneides* were inhabiting the area at the time the bay was formed and could have been isolated on the islands by the rising waters between 5,000 and 10,000 yrs ago.

Origin of the island populations by isolation would have certain general implications for their subsequent evolution. The populations would have been initiated with relatively large and representative gene pools. The opportunity for random genetic drift would have arisen only if the breeding populations were temporarily or permanently reduced to a size at which drift could occur. Further, they would have been isolated in association with a full complement of the plant and animal species of the local habitat, some of which survived the subsequent limitations of the island environment and some of which did not. The extinction of the latter would have been a non-random process in which species fates were determined by the absence of particular survival requirements in the island environments. The readjustment of the island communities would have been gradual, imposing progressive shifts of adaptive values in the surviving species populations. From these considerations it appears that evolutionary change in populations isolated in this way would be moderate and would take place slowly, other factors being equal.

Despite the evidence that the occurrence of *Batrachoseps* and *Aneides* in the area antedated the

formation of the bay, there are indications that at least some of the present island populations were established by waifs. This hypothesis is supported by the demonstration of the physiological possibility of transport on floating debris which was conducted in the laboratory. In other experiments (Anderson 1958) female *Batrachoseps* produced fertile clutches of eggs after three weeks of isolation, indicating that viable sperm may be retained by the females for a considerable period after mating. It appears that *Batrachoseps*, and probably *Aneides* also, is biologically capable of starting populations through the transport of a single gravid female.

The gene pool which would develop in a waif-established population could be expected to be quite different from that which would occur if a segment of the mainland population were cut off on the same island. Waif distribution is a process which has both random and highly selective components. The factors which determine the particular individuals of a species population which are carried into a body of water may be in part unpredictable; but habitat, breeding season, and individual differences in survival ability all act to select the individuals which reach an island. A population established by waifs would thus be initiated with genetic resources which represent a highly selected, as well as limited, portion of the gene pool of the parent population on the mainland. A significant aspect of such small initial gene pools has been discussed by Mayr (1954). He postulates that isolation of a small group of "founders" from which a larger population develops may possibly involve a change in the adaptive value of all genes present. This is because the genes must now operate upon a new, radically restricted, genetic substrate which is very different from that provided by the larger gene pool from which the founders were derived.

In addition to this founder effect, a population which owed its origin to two individuals only (as would be the case if a single gravid female were transported), or to a small group of waifs, would undergo an initial period of susceptibility to genetic drift. This susceptibility would exist as long as the growing population remained below a critical number of breeding individuals. This has been set by Simpson (1953) as high as 5,000 for a generalized situation. This means that the opportunity for drift would be somewhat proportional to the intrinsic rate of natural increase which is characteristic of the species. As an example, we may calculate that *Batrachoseps*, with a mean clutch size of 9 and a maximum life span of about 10 years, would require at least 12 annual generations to surpass this critical size. *Aneides*, with a similar life span and a mean clutch size of 21, would be theoretically capable of surpassing it in the 8th season of breeding and would be proportionately less subject to drift. Actual rates of population growth must be expected to fall well below the theoretical maximum and the opportunity for random loss or fixation during this initial growth period might be significant even in optimal habitats

on large islands. An experiment in which drift during the initial growth phase may have been a significant factor in the establishment of equilibria in laboratory *Drosophila* populations has been reported by Dobzhansky & Pavlovsky (1957). Their conclusion was that drift and selection interacted in determining evolutionary changes, selection operating on materials originally determined by drift. They suggested that such interaction may have produced the patterns of variation found in island butterfly populations by Dowdeswell & Ford (1952).

In the earliest phases of population growth random mortality may be an additional factor which plays a part in the determination of the gene pool. Since any mortality must be random with respect to most elements in the individual genotype, random loss of genes could result from the death of any individual in a very small population.

On the basis of the several factors discussed above it appears that origin of island populations through waif distribution favors divergence more than does origin by isolation of an established population.

Whatever its mode of origin, an island population which does not become extinct will eventually reach a size about which it will fluctuate. Assuming this size is such that drift does not fully control all loci, the population will be subject to a spectrum of selective forces determined by the interaction of its gene pool and the simplified island environment. It may be reasoned that the simplification of the island ecosystem will result in both direct and indirect alterations of adaptive values. Directly, selective forces may be altered in two ways. First, the absence of various predatory species, prey species, competitors, or other pertinent elements in the biotic environment, will eliminate the selective pressures they may have exerted. Second, selective forces which remain may be greatly intensified.

Two mechanisms seem capable of producing increases in intensity of selection in island environments. The first of these is the reduction in environmental diversity. During the course of its existence, an island population will harbor a variety of genotypes above that originally present. Some of these may result from recombinations, others from the introduction of truly new genetic material through mutation. Limits to the expansion of this variability may be imposed by the island environment, since islands will, in varying degree, lack the marginal habitats which would provide refugia for less well adapted individuals in a mainland situation. This is an effective increase in the intensity of selection. The phenomenon is probably illustrated by the reduction in the number of salamander-inhabited plant associations found on the bay islands (Table I). The reservoir of variability maintained in marginal environments might permit added evolutionary experimentation or prove invaluable in the face of major environmental changes. Dobzhansky (1957) has discussed these points in commenting on the relationship of the amount of adaptive polymorphism to the

environmental diversity, but feels that historical factors may have been more important in determining the composition of some of the island gene pools which he investigated.

A second effect of environmental simplification leading to intense selection may stem from the interaction of selective forces. In the complex matrix of the mainland environment one selective agent may be opposed or deflected in its action by other factors. The reduction in the number of predatory species affecting island *Batrachoseps* populations provides an illustration of this point. On the mainland, selection exerted by one of these predators may be countered by one or more of the others. For example, the coiling reaction which may protect the salamander from *Diadophis* predation to some extent could be detrimental when the animal is attacked by *Scapanus*. As another example, the predation which causes the high frequency of autotomy on Red Rock is probably much more influential in selection than it would be in a mainland situation. Selective forces may thus be buffered by each other, and it seems reasonable to expect that buffering effects are more the rule than the exception in mainland environments. The elimination of these buffering effects could greatly intensify the effectiveness of some of the selective forces active on the populations of small islands. Such changes in selection are in some ways an ecological analogue of the founder principle in genetics referred to above.

In view of the population responses which were discovered on Red Rock and Brooks Island, the simplification of island ecosystems may also have important indirect effects on natural selection. Referred to here are the results of reorganization of the mechanics of population control. In the present study, high population densities of *Batrachoseps* and *Aneides* were associated with small island size. Established features of the environments of such islands were a reduction in the number of predatory species and a loss of the opportunity to emigrate. The correlation of these features with high densities is interpreted as circumstantial evidence that predation and emigration play significant roles in the regulation of population size in mainland environments and that density has increased with the release of these controls. A reduction in clutch size, and an inhibition of reproductive activity in a significant proportion of the population, were also associated with the high densities. The mechanism connecting density to the latter phenomena remains to be clarified, but two levels of population control seem to be indicated. Control at the mortality level appears to be of greater importance in the mainland situations, while intra-populational factors, operating on the level of natality, seem to be brought into play by the high island densities. This adjustment cannot help but bring about a radical new alignment of adaptive values. It may tend, as well, to reduce the effective breeding population of small islands to levels at

which random drift may occur. In contrast, control at the mortality level requires a higher breeding population and tends to reduce the opportunity for drift, should the population be near the critical size. These indirect effects of the simplified island environments may be fully as important as the direct alterations of adaptive value discussed previously.

Waif origin of the island biota will tend to maximum simplification of the biotic portion of the ecosystem and thus will intensify these selective processes. The selective aspects of waif dispersal account for simplified community composition in the same way as they do for modifications in the species gene pools. The selective effects of waiving in this respect will be determined by various aspects of the biology of each potentially colonizing species. For example, the greater success of *Batrachoseps* in colonizing the bay islands can be attributed to its smaller size and the coincidence of the breeding season with the start of the heavy fall rains. *Aneides*, breeding in the late spring after the heavy rains are over, would have less chance of establishment by transport of a single gravid and fertilized female and would thus be less likely to initiate island populations than would *Batrachoseps*.

Irrespective of historical factors, the simplification of the ecosystem, and in particular its effects on population dynamics, are most intense on small islands. It may be an indication of the importance of these ecological factors that students of island populations (for example Lowe 1955, Kramer & Mertens 1938, Dobzhansky 1957, Ford 1956) have noted an inverse relationship between island size and the divergence of the isolated populations. On the basis of the foregoing discussion both drift and selection would be enhanced on small islands and the result in a specific instance might have been determined by either, or by the interaction of both as was suggested by Dobzhansky & Pavlovsky (1957).

Three points may be made in summing up the evolutionary aspects of small island environments. The first is that such environments are not merely different, but that they tend to differ in characteristic ways which seem capable of producing evolutionary change. Second, that certain of these evolutionary effects may be mediated through supra-individual aspects of populations, such as density. Third, that other effects may be mediated through such synthetic aspects of communities as their diversity. These latter two points suggest pathways by which evolution may tend toward the integration of both populations and communities as real units.

Isolation is a characteristic of all island populations, whatever their size or their origin. As has been pointed out in previous paragraphs, the isolating barrier may effect the evolution of island populations by filtering individuals or species reaching an island, and by preventing emigration, may contribute to high densities. Perhaps the most important function of isolation is the protective one dis-

cussed by Mayr (1954) and Ford (1956). These authors suggest that mainland populations can adapt to local conditions only to a limited degree because of the necessity of compromise with the genetic substrate favored by the range of habitats containing the species as a whole. Island populations are protected from infiltration by genes adaptive in other habitats and thus permit closer adjustment to local conditions. On this basis it appears that isolation would have a minor primary role in determination of the powerful evolutionary forces of the island environment and a major, but secondary, role in providing protection within which these forces may operate unimpeded by gene flow from other habitats.

The foregoing consideration of evolutionary forces operating on islands has been synthesized from the literature and from ideas derived as the result of observations reported in this study. Some tentative correlations may be attempted between these theories and the patterns of divergence disclosed in the morphological investigations. Red Rock represents the small island situation, conforming to the generalization that smaller islands show greater divergent tendencies. The environment is simplified and reduction in the number of interacting species (e.g. predators), high density, and adjustments in population dynamics have been demonstrated. The closer similarity of Red Rock *Batrachoseps* to the generalized mainland type, rather than to the populations of Brooks Island and Pt. Richmond, may indicate the original source of a waif established population, or a continuing arrival of waifs, sufficient to influence variation. Red Rock sits astride the major inflow of fresh water from the north as well as the course of a powerful tidal current sweeping up from the far south end of the bay. Probability of waif arrival from these directions may be higher than from nearby Pt. Richmond. The most probable summation of the evolution of the Red Rock *Batrachoseps* population seems to be that it is a long established population, perhaps of waif origin, and presently influenced by strong selective forces which may be interacting with drift as a result of the decline in effective breeding population brought on by high density.

The *Aneides* population on Red Rock is less divergent than the *Batrachoseps*, differing clearly from other populations in only one of the morphological characters investigated. This, together with the irregular occurrence of the species on the bay islands, suggests it may be of relatively recent waif origin. On the basis of population size and reproductive activity the opportunity for chronic, as contrasted with initial, genetic drift may exist, but no evidence in clear support of this hypothesis can be drawn from the morphological data at hand.

The *Batrachoseps* population on Brooks Island shows a close relationship with Point Richmond and considerable divergence from both Red Rock and the generalized mainland type. The island does not

lie in the direct path of the fresh water inflow, nor of the tidal currents, which seem to have influenced the Red Rock population. If waif transport has occurred, the most probable route lies across the protected waters between the island and the nearby mainland areas. Population size seems sufficient to eliminate the possibility of chronic drift, despite reproductive inhibition and any effects of the changes in population dynamics must be mediated by selection.

On the basis of present land contours it appears that Point Richmond and Brooks Island might have been joined at a time when both were isolated from the mainland. If this were the case the affinities of the Point Richmond and Brooks Island populations to each other are indicative of a common ancestral population which was isolated by the rising waters and underwent an evolutionary divergence from the mainland form. Further sea level rise might then have separated Brooks Island and Point Richmond while sedimentation built toward the connection of the latter with the mainland. When human enterprise led to the completion of this new connection about 40 yrs ago the Pt. Richmond population was able to invade the mainland and interbreed with mainland populations. This hypothesis is supported by the intermediate position and high variability of the Berkeley population and a detailed study of the mainland variation patterns of the east side of the bay should be made to determine its validity. Mayr (1954) has suggested that islands peripheral to continents may be important incubators for new gene pools which eventually invade the mainland and initiate new evolutionary lines. The Pt. Richmond and Berkeley populations strongly suggest that such an invasion is going on.

The *Aneides* population of South Farallon island seems to have diverged from nearby mainland populations only in number and size of the yellow spots. An occasional individual in mainland populations around the bay will display spotting similar to that seen in Farallon animals, and populations along the southern edge of the Salinas valley, 100 mi to the south, show a similar spotting generally. The Farallon population probably originated through the transport of one or two individuals to the island. Presently available data give no clues as to whether these may have come from the nearby mainland or from the area south of the Salinas valley, but careful study of the latter population might solve this problem.

SUMMARY

Populations of *Aneides lugubris* and *Batrachoseps attenuatus* occur on islands in and near San Francisco Bay. These islands range in area from 3 to 1100 acres. Analyses indicate that the island ecosystems are highly simplified. The degree of simplification is related to size, topography, and isolation, and can be shown to influence the ecological

relationships of the salamanders in such respects as predation, diet, and diversity of available habitat.

The islands of the bay itself were formed as the result of sea level changes at the end of the Pleistocene. Fossil and distributional evidence indicates that the salamanders occurred in the area prior to the formation of the islands. Patterns of distribution and variation suggest that some populations were isolated by the rising waters, while others were established by waifs. Survival of individuals under conditions to be expected during waif dispersal was experimentally demonstrated.

Salamander populations on the islands show divergence from the mainland in several aspects of population ecology. On two of the smaller islands, which were intensively studied, very high densities were found. Associated with these high densities were shifts in age structure, there being unusually high proportions of older individuals. Such age structure implies low mortality and low natality. Investigation of reproductive activity showed the age structure shifts were correlated with inhibition of reproduction. In female *Batrachoseps*, inhibition was of two types, juvenilization of the gonads, and failure of animals with mature oocytes to oviposit. Male *Batrachoseps* showed less evidence of inhibitory effects. Female *Aneides* showed a tendency towards underdeveloped gonads at high population densities, as did males, but the effects were not so dramatic as in *Batrachoseps* females. It appears that reproductive inhibitions resulting from high density may so affect the breeding size of small populations that genetic drift is likely. In addition to inhibition of reproductive activity, island populations showed significant reduction in clutch size as compared with the mainland, with different mechanisms indicated for the two species studied. These phenomena suggest that high density has resulted in a shift in the means of population control, emphasizing those mechanisms operating at the natality level.

In an analysis of morphological variation no significant reduction in coefficients of variation was found in island populations. Comparison of island and mainland populations showed a tendency to divergence on the part of the former which must be considered impressive in view of the conservative evolutionary tendencies of these species on the mainland. Divergence between island and nearby mainland populations shows an inverse relationship to island size, irrespective of the degree of isolation, and therefore is directly correlated with the intensity of the ecological factors described. Variation patterns support the hypothesis that some populations may be waif-established. The relationship of the *Batrachoseps* populations of Brooks Island, Pt. Richmond, and Berkeley suggests that the former two have shared a common island evolution and have been separated relatively recently, while the very recent connection of Pt. Richmond with the mainland has

resulted in significant modification of the mainland gene pool along the eastern shore of the bay.

Consideration of the data gathered, in relation to a generalized theory of evolution on islands, leads to the suggestion that the role of isolation is largely protective, permitting the unimpeded operation of powerful evolutionary forces characteristic of island environments. Among these are the restriction of the genetic and ecological substrates upon which the population exists. Restriction of the genetic substrate (the "founder principle") confers new adaptive value on all genes present irrespective of any environmental changes. Restriction of the ecological substrate has an analogous effect on selective forces. An important aspect of this may be the absence of the buffering effects of counter selection which are thought to exist in complex mainland environments, and thought to be reduced as a result of simplification of the island ecosystems. Another result of this simplification is the development of high population densities. These result in compensatory reactions (e.g. reproductive inhibition) leading to the utilization of new population control mechanisms and, therefore, to new modes of selection. On small islands such responses may reduce effective breeding populations to levels where drift may occur. Operation of the ecological factors, and of the "founder principle" will be most extreme where island communities develop as the result of waif dispersal. The interaction of the various factors is complex, but the data presented suggest that island populations lend themselves to studies which will contribute much to our understanding of evolutionary mechanisms.

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ECOLOGICAL RELATIONSHIPS OF *PEROMYSCUS LEUCOPUS* *NOVEBORACENSIS* AND *P. MANICULATUS* *GRACILIS* IN CENTRAL NEW YORK

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INTRODUCTION

The ecological relationships of the deer mice, *Peromyscus leucopus noveboracensis* (Fischer) and *P. maniculatus gracilis* (Le Conte), have been of some interest to workers in the past. These forms occupy very similar ecological niches; they are both essentially forest-dwelling deer mice and apparently have similar food habits. Hamilton (1941) made no distinction between the two in this regard, and Cogshall (1928) found their food preferences in the laboratory to be very similar. They are also similar in size and morphology, so much so that it is often difficult to identify specimens, particularly immature ones.

Various authors have commented on the ecological distribution of the two animals. In his revision of the genus *Peromyscus*, W. H. Osgood (1909) said, "Although living in the same general localities, *gracilis* and *noveboracensis* are nearly always confined to different local habitats, *gracilis* showing preference for the colder, more moist places, or deep, mostly coniferous, woods; *noveboracensis* for the warmer, dryer, more open country, or deciduous woods." Others have noted differences in distribution related to habitat or elevation (Gunderson & Beer

1953, Hamilton 1943, Osgood 1938, Rhoads 1903, Swanson, Surber & Roberts 1945). Priddy (1942) and Jameson (1949) collected both forms from the same study areas in central New York, although *P. m. gracilis* was much less abundant and more restricted in its distribution than *P. l. noveboracensis*.

P. m. nubiterrae replaces *P. m. gracilis* along the Appalachian Mountain chain southward from western New York. Workers in this area have generally reported that *P. m. nubiterrae* occurs at higher elevations and in cooler, moister habitats than *P. l. noveboracensis* (Handley & Patton 1947, Kellogg 1937, 1939, Barbour 1951, Odum 1949).

In central New York, where the geographic ranges of *P. m. gracilis* and *P. l. noveboracensis* overlap, the altitudinal range is about 125-610 m (410-2000 ft). *P. m. gracilis* is more restricted in its distribution than *P. l. noveboracensis* and this appears to be correlated with altitude. However, both forms may be collected in the same woodland areas. This situation is of interest in connection with Gause's "hypothesis" (Gilbert, Reynoldson & Hobart 1952) that two species with the same ecology cannot live together in the same place. With this in mind, a study was undertaken to investigate the ecological relations of the two species in the woodlands they occupied in central New York.

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for their helpful advice during the study, and for their guidance in preparation of the manuscript. D. S. Robson gave advice on the statistical estimation of populations of mice.

STUDY AREAS

Ecological studies were conducted on three woodland areas near Ithaca, Tompkins County, in central New York. The areas were selected on one or both of the following bases: (1) *Peromyscus leucopus noveboracensis* and *P. maniculatus gracilis* had been reported from the general area and (2) the diverse kinds of woodland vegetation indicated by Osgood (1909) were present. These included *Tsuga canadensis* (hemlock) and *Quercus Prinus* (chestnut oak), *Q. borealis* (red oak) or *Q. alba* (white oak). (Plant nomenclature is that of Clausen 1949.)

SMILEY'S WOODS

This study area was located 8.9 km (5.5 mi) east-northeast of Ithaca at latitude 42°27' 37", longitude 76° 24' 2". Altitudinal range of the area was about 380-410 m. It was situated on a moderate north-facing slope, the northwest side of Mt. Pleasant, a hill rising to 534 m. A stream and an intermittent watercourse traversed the study area in a northerly direction, and dissection of the area by this drainage pattern caused fairly steep east and west-facing slopes. The stream was located on the eastern edge of the trapping grid. Some *Tsuga canadensis* trees were located toward this edge of the study area. The remainder of the area was covered with second-growth *Fagus grandifolia* (beech) and *Acer nigrum* (sugar maple) woods. (Following Clausen (1949), the name *Acer nigrum*, as used in this work, signifies the aggregate of all the sugar maples.) Old trails ran alongside the stream and the water-course. Some cutting of timber had been done on the eastern part of the area and sapling trees grew there. Along the stream the tree canopy was fairly open, accounting for some of the denser ground cover found there.

CONNECTICUT HILL

This study area was situated 17.9 km southwest of Ithaca at latitude 42° 21' 23", longitude 76° 40' 34". The altitudinal range of the area was about 565-595 m. The trapping grid was situated on the upper east slope of a hill, the top of which had once been cultivated. This hilltop area had now grown up with *Pinus Strobus* (white pine) and deciduous trees which had not yet formed a closed canopy. The western part of the grid was mostly covered with *Quercus Prinus*, *Q. borealis* and *Acer rubrum* (red maple) trees. The eastern part contained more *Tsuga canadensis*, *Fagus grandifolia* and *Acer nigrum*. Some cutting had been done on the area several decades previously, and part of it was covered with a dense growth of sapling trees.

ARNOT FOREST

The Arnot Forest study area was located 22.7 km south-southwest of Ithaca at latitude 42° 17' 30", longitude 76° 40' 00". Altitudinal range of the area was 505-550 m. The trapping grid was bisected by a westward-flowing watercourse. The northern part of the trapping grid was located on a steep, dry, southwest-facing slope clothed with *Quercus Prinus* and *Pinus Strobus* trees. The southern part of the grid ran partway up a steep, moist, north-facing slope covered with *Acer nigrum*, *Fagus grandifolia* and *Tsuga canadensis* trees. The middle part of the grid occupied a fairly flat stream valley floor which sloped moderately to the west. Part of this area was covered with a heavy growth of *Tsuga canadensis*. Other parts of this area were covered with *Fagus grandifolia*, *Acer nigrum*, *A. rubrum* and *Fraxinus americana* (white ash) trees.

METHODS

TRAPPING STUDIES

Trapping grids on each area were laid out by pacing, with the aid of a compass. The interval between trap stations in each line and between lines was about 14 m (45 ft).

Single-catch live-traps used were constructed of 0.8-cm (5/16 in) mesh hardware cloth. Trap dimensions were 31 x 7 x 7 cm. A treadle arrangement released a downward-swinging door which latched shut upon falling.

Mark-and-recapture studies were carried out on each of the areas during the summers of 1955 and 1956. They were usually conducted for about two weeks on each area. Mice were marked individually by clipping a toe on both a forefoot and a hindfoot. This allowed for the identification of 80 mice on each area. At the end of the live-trapping program, the areas were generally snap-trapped to recover marked individuals for more thorough identification and for the basis of population estimation. During the summer of 1957, brief snap-trapping programs of two consecutive nights were carried out on each of the areas. Table 1 contains a summary of the number of trapping stations operated each year on each area and of the number of nights the stations were operated. In 1955, trapping grids were small and during each trapping night one trap was set at each station on the grid. Figs. 1, 2 and 3 are diagrams of trapping grids for the study area in 1955, showing sex and number of individual deer mice trapped at each station. In 1956, the trapping grids were much enlarged and a different scheme of operating the trap stations was used. The trapping grid was divided into units consisting of four adjacent trap stations in a square. Only one station per unit of four was operated during a trapping night and two traps were set at this station. During a trapping period, selection of the station to be operated for a trapping night was made with a table

of random numbers. However, the same station was not operated on consecutive trapping nights, and some subjective choice of station was made to insure that each station was operated a fair number of times. The effect of this procedure was to increase the distance between traps in order to allow a mouse to cover more of its home range before encountering a trap. It also tended to eliminate repeated captures of a mouse at a station due to its having learned of a ready source of food. Trapping grids for 1956 are diagrammed in Figs 4, 5, and 6.

TABLE 1. Summary of number of trapping stations, number of trapping nights and total area sampled by trapping grid for three study areas, 1955 through 1957.

| | Smiley's Woods | | | Connecticut Hill | | | Arnot Forest | | |
|-------------------------|----------------|------|------|------------------|------|------|--------------|------|------|
| | 1955 | 1956 | 1957 | 1955 | 1956 | 1957 | 1955 | 1956 | 1957 |
| No. of stations..... | 60 | 120 | 120 | 60 | 140 | 140 | 44 | 163 | 163 |
| No. of nights..... | 12 | 16 | 2 | 11 | 16 | 2 | 6 | 17 | 2 |
| Area sampled, acres.... | 6.6 | 10.6 | 10.6 | 6.8 | 12.0 | 12.0 | 6.0 | 15.3 | 15.3 |
| Area sampled, hectares. | 2.7 | 4.3 | 4.3 | 2.8 | 4.9 | 4.9 | 2.4 | 6.2 | 6.2 |

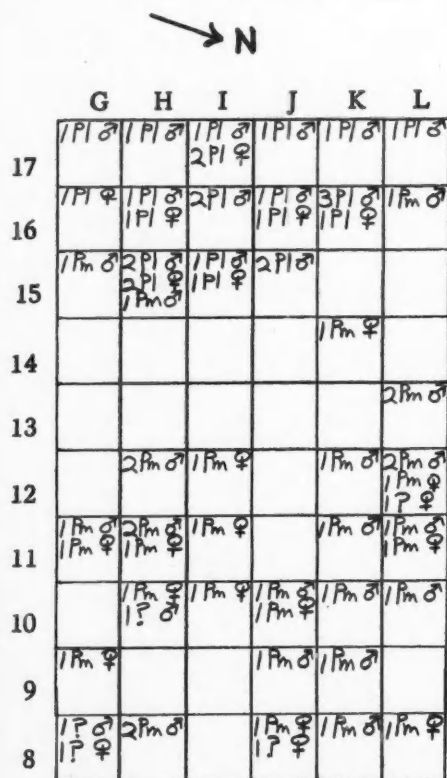


Fig. 1. Diagram of 1955 Smiley's Woods study area showing sex and number of different individuals of each species trapped at each station. Closed squares represent trapping stations. Question marks indicate unidentified individuals. Pl = *Peromyscus leucopus noveboracensis*; Pm = *Peromyscus maniculatus gracilis*.

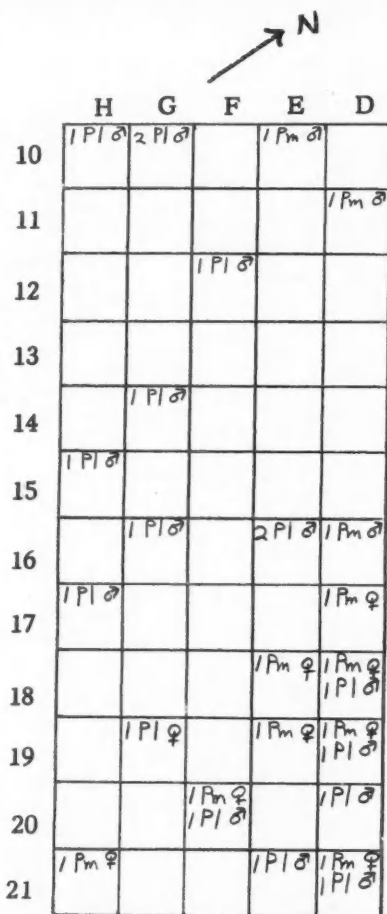


Fig. 2. Diagram of 1955 Connecticut Hill study area. Details as in Fig. 1.

VEGETATION STUDIES

The primary method of investigating the ecology of the two species of *Peromyscus* was through a vegetational analysis of the areas occupied by mice of each form. Two approaches were used. One involved the use of sample plots at trap stations visited by mice. All of the visited stations were not sampled because of lack of time. Stations selected were those at which the largest number of different individuals were trapped, or which had the largest number of recaptures of mice. An effort was also made to distribute the sample plots as evenly as possible over the trapping grid. Tree, shrub and ground strata of the vegetation were analysed by recording the estimated percentage of cover of each species on the plot according to a coding scheme adapted from Domin (1923) by R. T. Clausen. For purposes of summarizing and averaging the percentage of cover of each plant species, a representa-

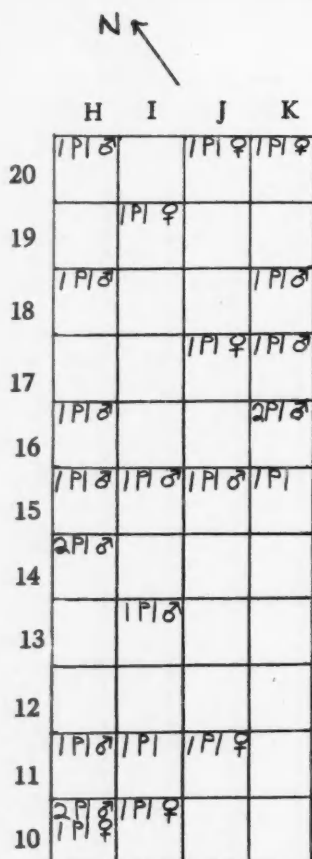


Fig. 3. Diagram of 1955 Arnot Forest study area. Details as in Fig. 1.

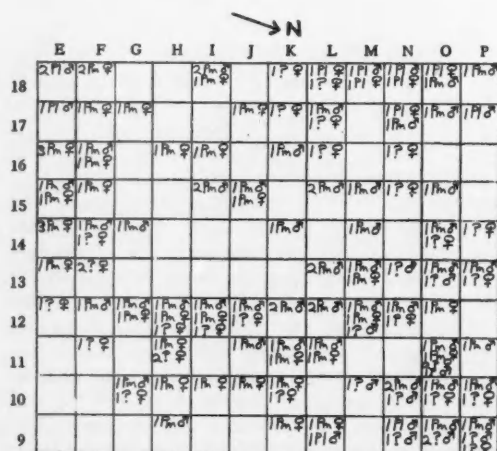


Fig. 4. Diagram of 1956 Smiley's Wood study area. Details as in Fig. 1.

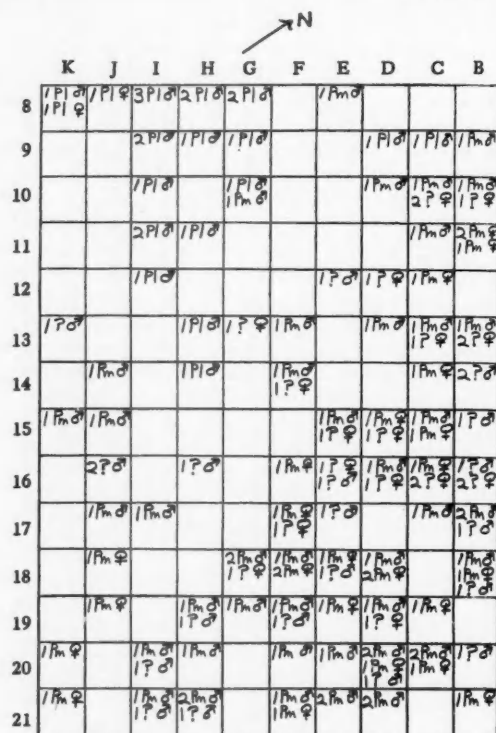


Fig. 5. Diagram of 1956 Connecticut Hill study area. Details as in Fig. 1.

TABLE 2. Classification used for noting amount of cover of the vegetation on sample plots.

| Cover category | Percentage of cover | Representative value |
|----------------|---------------------|----------------------|
| 1..... | Less than 1 | 0.5 |
| 2..... | Approximately 1 | 1.0 |
| 3..... | 2 to 10 | 5.0 |
| 4..... | 11 to 20 | 15.0 |
| 5..... | 21 to 50 | 35.0 |
| 6..... | 51 to 75 | 63.0 |
| 7..... | 76 to 100 | 87.0 |

tive value for each cover category was selected (Table 2).

Sample plot sizes were: (1) For the ground layer of vegetation (herbaceous and woody) less than 0.5 m high, 4.6 x 1.5 m, covering an area of 6.9 sq m; (2) For the shrub layer of vegetation 0.5 to about 3.7 m high, 8.2 x 2.7 m, covering an area of 22.1 sq m; (3) For the tree layer of vegetation taller than 3.7 m, 10.1 x 3.4 m, covering an area of 34.3 sq m. The number of sample plots for each area was 60 at Smiley's Woods, 64 at Connecticut Hill and 101 at Arnot Forest. All plots were analysed during the summer of 1956 except for some in Smiley's Woods

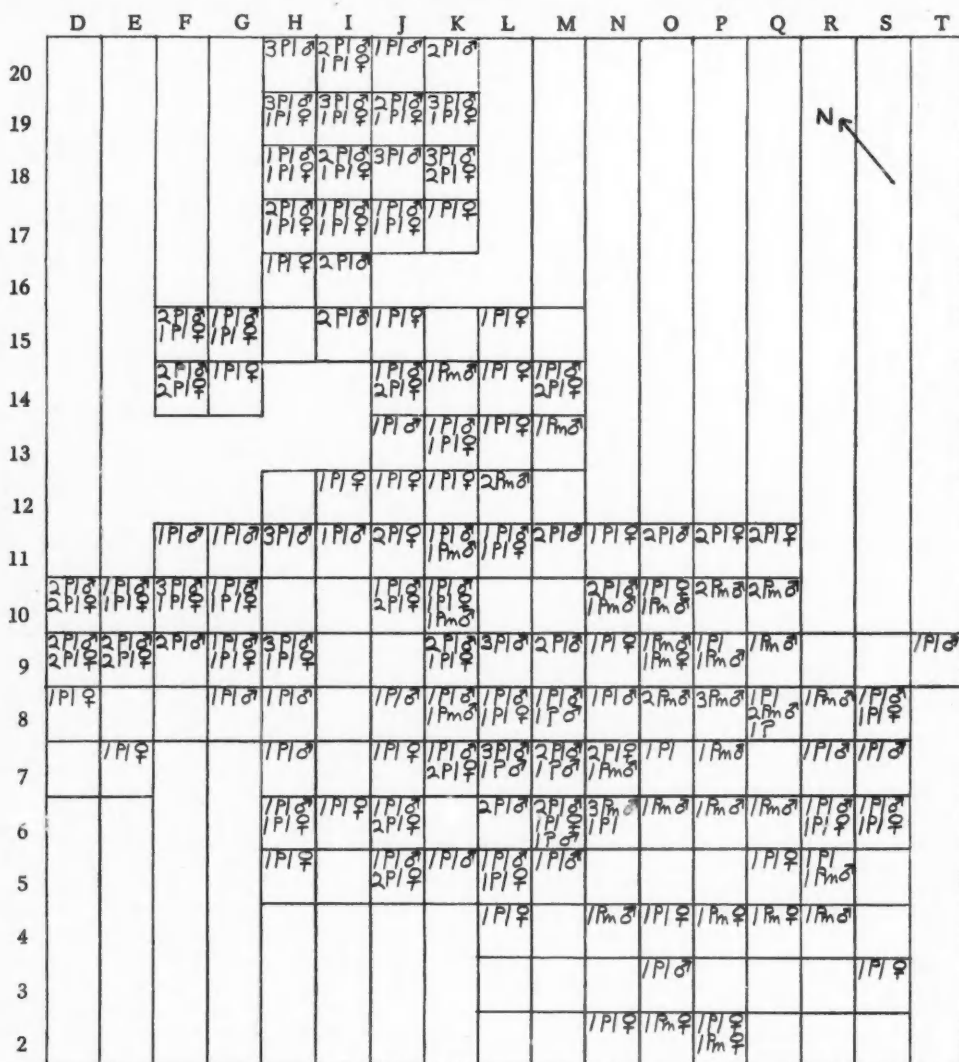


Fig. 6. Diagram of 1956 Arnot Forest study area. Details as in Fig. 1.

which were done during 1955. Although trapping data were obtained from 1955 through 1957, the vegetation seemed to be stable enough to rely on a single sampling of the vegetation for correlation with the trapping data.

The other method of vegetation analysis noted the presence or absence at each trapping station of selected species of plants which were presumed to be significant as indicators of ecological conditions. These data were collected during the summers of 1956 and 1957. Plant species were selected on the basis of their known or observed affinity for various habitats which ranged from warmer, drier habitats of south and west-facing slopes to cooler, moister hab-

itats of north and east-facing slopes. These species and their abbreviations are listed in Table 3. They have been categorized according to whether they are typical of the Hemlock-White Pine-Northern Hardwoods Forest region or of the Oak-Chestnut Forest region of Braun (1950). These vegetational data were combined with trapping data on the presence or absence of individuals of *P. m. gracilis* or *P. l. noveboracensis*. The combined data were used to obtain coefficients of interspecific association between animal and plant species (Cole 1957). Also recorded at each station was the estimated percentage of cover of all the vegetation in the ground layer, and the kind of humus present, mull or mor.

TABLE 3. Names and abbreviations of plant species typical of the Hemlock-White Pine-Northern Hardwoods Forest and the Oak-Chestnut Forest regions. Nomenclature after Clausen (1949).

| Abbreviation | Scientific and common names of species included |
|--|---|
| I. Plant species typical of the Hemlock-White Pine-Northern Hardwoods Forest region. | |
| A. T.B.A. | A. (1) <i>Tsuga canadensis</i> (hemlock) (2) <i>Betula lutea</i> (yellow birch) (3) <i>Acer pennsylvanicum</i> (striped maple) |
| B. P.D.D.D. | B. (1) <i>Polystichum acrostichoides</i> (Christmas fern) (2) <i>Dryopteris noveboracensis</i> (New York fern) (3) <i>D. spinulosa</i> (spinulose shield fern) (4) <i>D. marginalis</i> (marginal shield fern) |
| C. F.g. | C. <i>Fagus grandifolia</i> (beech) |
| D. A.n. | D. <i>Acer nigrum</i> (sugar maple) |
| II. Plant species typical of the Oak-Chestnut Forest region. | |
| A. Q.a. | A. <i>Quercus alba</i> (white oak) |
| B. Q.b. | B. <i>Q. borealis</i> (red oak) |
| C. R.V.G.P. | C. (1) <i>Rhododendron nudiflorum</i> (pink azalea) (2) <i>Vaccinium angustifolium</i> (upland blueberry) (3) <i>Gaultheria procumbens</i> (winterberry) (4) <i>Pteridium aquilinum</i> (bracken fern) |
| D. Q.P. | D. <i>Quercus Prinus</i> (chestnut oak) |

RESULTS

TRAPPING DATA

Table 1 summarizes data concerning the area sampled by trapping grids each year. The areas actually covered by the trapping grids were in each case slightly smaller than the areas shown as sampled in the table. The increased area is due to a band around the trapping grid from which mice may travel to reach the traps. The width of this peripheral area is an unknown factor in determining the total area from which a trapping grid may be capturing animals. It is dependent upon the dimensions of the home ranges of the individuals living in the study area and has usually been assumed to be one-half the diameter of the home range (Dice 1938 and others). Stickel (1946) stated that a peripheral band this wide would cause increasing areal inaccuracies with increase in area studied; she suggested dividing the mean range (or movement) diameter between the inside and the outside of the periphery of the trapped area. The mean diameter should be proportioned so that the band described by the outside member is equal in area to the band described by the inside member.

The method used in the present study is a modification of that advocated by Dice (1938) who used the square root of the home range area as the mean width of the home range. In this study, the figure for the linear dimension of a home range (actually, merely recorded movements of an animal during the trapping period, as pointed out by Stickel 1946) was obtained by averaging the maximum and minimum dimensions of the observed home range. This procedure is diagrammed in Fig. 7. The two most distant stations are selected and the points half-way to the next station are established (A and B). Ex-

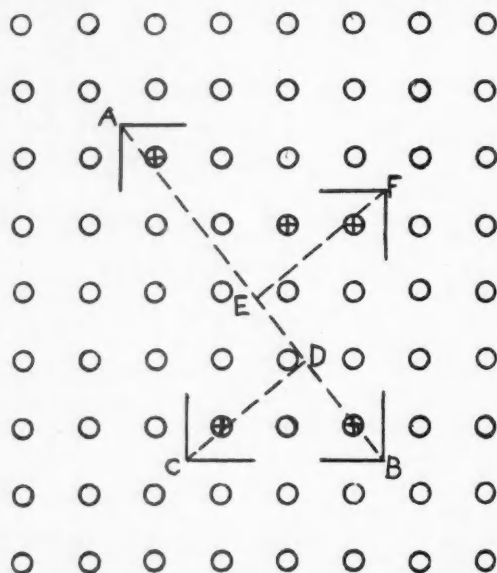


Fig. 7. Diagram showing method used to measure dimensions of an individual home range. Circles represent trapping stations. Crosses represent captures of an individual mouse.

tension of home range dimensions to one-half the distance to the next trap station has been shown by Stickel (1954) (in experiments with model home ranges) to give better approximations of range dimensions and area, than calculations based on home range dimensions measured only to the peripheral trap stations. The distance AB is measured as the maximum dimension. Perpendiculars (CD and EF) are extended on either side of AB to the stations (plus half the distance to the next station) farthest from AB. These lines are measured and their dimensions added, to become the minimum dimension of the home range. The maximum and minimum dimensions are then averaged to give the mean linear dimension of the home range.

Since non-circular home ranges may be oriented in any fashion with respect to the edge of the trapping grid, a mean linear dimension seems to give an average expression of the extent to which home ranges in various positions at the edge of a trapping grid may extend beyond this border line. One-half of such a mean linear dimension has been obtained from the calculated home ranges of 29 *Peromyscus leucopus noveboracensis* and 31 *P. maniculatus gracilis* individuals of both sexes, which had been captured at 4-11 different stations. This value was 36.9 m. An area this wide was added around the periphery of each trapping grid to yield the values for "Area sampled" in Table 1. Differences between areas, species and sexes did not appear to be sufficiently great to warrant calculating separate mean linear dimensions.

Table 4 summarizes the numbers of *P. l. noveboracensis*, *P. m. gracilis* and unidentified individuals trapped on the study areas and considered resident on the areas. The 1955 and 1956 animals were obtained by live-trapping, and the 1957 animals by snap-trapping. Unidentified individuals resulted from a failure to recover marked mice at the end of live-trapping programs. It proved difficult in many instances to identify mice in the live-traps. Study areas were snap-trapped after the live-trapping programs in order to recover marked individuals for more positive identification. In a few instances, notably at Connecticut Hill in 1956, many marked mice were not recovered during intensive snap-trapping programs. These individuals could not be used in ecological studies of the areas and are indicated by question marks in Figs. 1, 4, 5 and 6.

TABLE 4. Summary of *P. l. noveboracensis* (P. l.), *P. m. gracilis* (P. m.) and unidentified *Peromyscus* on three study areas, 1955 through 1957.

| | Smiley's Woods | | | Connecticut Hill | | | Arnot Forest | | |
|--------------|----------------|------|------|------------------|------|------|--------------|------|------|
| | 1955 | 1956 | 1957 | 1955 | 1956 | 1957 | 1955 | 1956 | 1957 |
| P.l..... | 5 | 5 | 4 | 7 | 5 | 2 | 12 | 49 | 3 |
| P.m..... | 10 | 19 | 6 | 2 | 16 | 6 | 0 | 15 | 5 |
| Unident..... | 2 | 7 | 0 | 0 | 17 | 0 | 0 | 2 | 0 |

In most of the live-trapping programs it is probable that all the resident mice on an area were marked during the course of the study. In three cases an unmarked mouse was taken on the last day of the live-trapping period, indicating the possibility that all the resident mice had not been captured, or that mice were moving into the area. The last possibility may have been occasioned by the death of resident mice by trapping. However, on only one area is it definitely known that two mice died as a result of trapping.

A Petersen (1896) population estimate was calculated for each live-trapping program. Captures from the last night of live-trapping were used as the sample from which the ratio of marked individuals to total number caught was observed. In addition, the unidentified individuals were partitioned between the two species according to the proportion of each in the total number of identified mice. Table 5 contains the estimated number of each form on each study area. Also noted are the estimated numbers per acre, and the total number of all mice per acre for 1955 and 1956. The areal bases for these density calculations are the data for "Area sampled" in Table 1. Mouse densities based on preferred habitat were not objectively obtainable because of a lack of definite knowledge of the nature of preferred habitat for each form.

TABLE 5. Summary of population estimates and density of *P. l. noveboracensis* (P. l.) and *P. m. gracilis* (P. m.) on three study areas, 1955 and 1956.

| | Smiley's Woods | | Connecticut Hill | | Arnot Forest | |
|---------------------------------|----------------|------|------------------|------|--------------|-------|
| | 1955 | 1956 | 1955 | 1956 | 1955 | 1956 |
| Est. no. P.l. on area..... | 6 | 6 | 7 | 10 | 12 | 51 |
| Est. no. P.m. on area..... | 12 | 25 | 2 | 30 | 0 | 15 |
| Est. no. P.l. per acre..... | .91 | .57 | 1.03 | .83 | 2.00 | 3.33 |
| Est. no. P.m. per acre..... | 1.82 | 2.36 | .29 | 2.50 | 0.00 | .98 |
| Total no. mice per acre..... | 2.73 | 2.93 | 1.32 | 3.33 | 2.00 | 4.31 |
| Est. no. P.l. per hectare..... | 2.22 | 1.40 | 2.50 | 2.04 | 5.00 | 8.23 |
| Est. no. P.m. per hectare..... | 4.44 | 5.81 | .71 | 6.12 | 0.00 | 2.42 |
| Total no. mice per hectare..... | 6.66 | 7.21 | 3.21 | 8.16 | 5.00 | 10.65 |

INTERSPECIFIC RELATIONSHIPS OF

P. l. noveboracensis AND *P. m. gracilis*

A method for the statistical analysis of the distribution of two or three species has been worked out by Cole (1957). Data from collections can be used in the method to yield a coefficient of interspecific association. This statistic may range from -1.00, indicating complete negative association of species, to +1.00, indicating complete positive association. A value of 0 indicates that the species are distributed at random to each other, and are not positively or negatively associated. This method may be used to analyze the association of two species alone, or of two species in the presence and absence of a third species or factor. The former variation was applied to trapping data from study areas of 1955 and 1956. Presence of an individual at a trap station at any time during the trapping period counted for a positive occurrence of the species at that station.

Table 6 contains the coefficients of association of *P. l. noveboracensis* and *P. m. gracilis* for five trapping periods during which both forms were present. Statistical tests for significance can be applied to data used in the method. During three trapping periods, the two mice were negatively associated to a fairly high degree, with high statistical significance. Data from the other two trapping periods were not statistically significant. Small numbers of one or the other form were responsible.

TABLE 6. Coefficients of interspecific association between *P. l. noveboracensis* and *P. m. gracilis* for five trapping periods. Asterisks indicate statistical significance at the 1% level.

| | Smiley's Woods | | Connecticut Hill | | Arnot Forest |
|------------------|----------------|------|------------------|--------|--------------|
| | 1955 | 1956 | 1955 | 1956 | 1956 |
| Coefficient..... | -.84** | -.31 | +.15 | -.82** | -.43** |

Although data arising from this method may be used to detect possible antagonism between individuals of two species, in this case the negative coefficients do not appear to have been caused primarily by

this factor. By inspecting Figures 1, 4, 5 and 6 it may be seen that, in general, identified individuals of each species were grouped together in different parts of the trapping grid. Unidentified individuals have not, of course, entered into the calculation of the coefficients. In the Smiley's Woods area, 1956, and in the Connecticut Hill area, 1956, the majority of the unidentified animals (in the lower parts of Figures 4 and 5, respectively) were believed to be *P. m. gracilis*. Tentative assignment of at least most of the unidentified animals to *P. m. gracilis* preserves the general pattern of distribution of the two species on each area, as outlined above.

In the Arnot Forest 1956 trapping grid covered by lines N through T, both forms appeared to be living together in relatively equal numbers (19 *P. l. noveboracensis* and 14 *P. m. gracilis*) and with about the same activity. *P. l. noveboracensis* individuals were trapped 38 times and *P. m. gracilis* individuals 37 times. In 13 instances, both traps at a station were occupied on the same night. On the basis of the near equal number of captures of individuals of each form, the expected proportions of P.l. - P.l., P.m. - P.m. and P.l. - P.m. double captures were calculated. A chi-square statistical test indicated no significant deviation of observed from expected values. In addition, 19 stations were categorized according to whether only *P. l. noveboracensis*, only *P. m. gracilis* or both had been trapped at them at any time during the period. A chi-square test indicated that observed values did not differ significantly from the expected. It appears that in this area, where home ranges of individuals of the two species overlapped, the occasions when both were represented at one trap station in one night, and the number of trap stations at which members of both forms were taken during the period, did not differ from expectation in a random distribution of individuals. For this part of the Arnot Forest study area, the coefficient of association between the two forms was not statistically significant.

Some observations were made in captivity on the reactions of two newly introduced mice. Combinations observed were of the same and of different species, and within these combinations, pairings of the same and of opposite sexes. Although only about 15 pairings were observed, the behavior of two mice of unlike species appeared to be no different than that of mice of the same. In most cases there was antagonism, or at least caution, displayed by individuals when first put together. This usually quickly disappeared, and animals that were kept together for long periods usually occupied the same nest and huddled together. No instances of cannibalism occurred under these circumstances. From these limited observations, it appears that individuals do not exhibit an antagonism which would cause them to drive members of the other species from their home ranges.

ECOLOGICAL STUDIES OF PEROMYSCUS SPECIES IN RELATION TO VEGETATION

Sample plot studies.—Trapping data for 1955 and 1956 were used with data from sample plot

TABLE 7. Summary of sample plot data for the tree layer of vegetation at Smiley's Woods and Connecticut Hill, 1955 and 1956. Sample plots summarized according to the species of *Peromyscus* trapped at the station. F, % frequency of occurrence of a plant species in the sample plots. C, average % cover of a plant species over all sample plots in a mouse species group. Zero values for F indicate that the species was found on the study area but not in the sample plots.

| Smiley's Woods | | | | | | | | | |
|------------------------------------|------------|----|------------|----|------------|----|------------|----|--|
| Number of plots | 1955 | | | | 1956 | | | | |
| | P.l. plots | | P.m. plots | | P.l. plots | | P.m. plots | | |
| | 9 | | 20 | | 9 | | 49 | | |
| | F. | C. | F. | C. | F. | C. | F. | C. | |
| <i>Acer nigrum</i> | 100 | 22 | 90 | 21 | 100 | 25 | 94 | 23 | |
| <i>A. pennsylvanicum</i> | 33 | 2 | 15 | 1 | 22 | 0 | 18 | 1 | |
| <i>A. rubrum</i> | 33 | 5 | 5 | 1 | 0 | 0 | 16 | 2 | |
| <i>Betula lenta</i> | 78 | 9 | 20 | 3 | 33 | 11 | 39 | 6 | |
| <i>B. lutea</i> | 0 | 0 | 20 | 1 | 0 | 0 | 16 | 1 | |
| <i>Carpinus caroliniana</i> | 0 | 0 | 25 | 2 | 22 | 1 | 16 | 1 | |
| <i>Carya glabra</i> | 0 | 0 | 15 | 1 | 11 | 0 | 4 | 0 | |
| <i>C. ovata</i> | 0 | 0 | 20 | 1 | 11 | 1 | 8 | 0 | |
| <i>Fagus grandifolia</i> | 100 | 56 | 65 | 10 | 78 | 26 | 86 | 30 | |
| <i>Fraxinus americana</i> | 11 | 0 | 35 | 4 | 44 | 4 | 33 | 3 | |
| <i>Hamamelis virginiana</i> | 0 | 0 | 10 | 0 | 0 | 0 | 6 | 0 | |
| <i>Magnolia acuminata</i> | 22 | 1 | 10 | 1 | 0 | 0 | 10 | 0 | |
| <i>Ostrya virginiana</i> | 67 | 6 | 55 | 5 | 67 | 6 | 50 | 4 | |
| <i>Populus grandidentata</i> | 0 | 0 | 10 | 3 | 0 | 0 | 8 | 1 | |
| <i>Prunus pensylvanica</i> | 0 | 0 | 5 | 0 | 0 | 0 | 4 | 0 | |
| <i>P. serotina</i> | 0 | 0 | 25 | 3 | 11 | 2 | 10 | 1 | |
| <i>Quercus borealis</i> | 56 | 2 | 15 | 2 | 11 | 1 | 20 | 1 | |
| <i>Tilia americana</i> | 33 | 7 | 90 | 14 | 67 | 16 | 59 | 8 | |
| <i>Tsuga canadensis</i> | 0 | 0 | 70 | 18 | 11 | 1 | 39 | 9 | |

| Connecticut Hill | | | | | | | | | |
|------------------------------------|------------|----|------------|----|------------|----|------------|----|--|
| Number of plots | 1955 | | | | 1956 | | | | |
| | P.l. plots | | P.m. plots | | P.l. plots | | P.m. plots | | |
| | 15 | | 8 | | 14 | | 43 | | |
| | F. | C. | F. | C. | F. | C. | F. | C. | |
| <i>Acer nigrum</i> | 73 | 19 | 75 | 21 | 57 | 12 | 81 | 15 | |
| <i>A. pennsylvanicum</i> | 20 | 2 | 38 | 2 | 0 | 0 | 23 | 2 | |
| <i>A. rubrum</i> | 33 | 7 | 25 | 9 | 86 | 21 | 47 | 11 | |
| <i>Amelanchier</i> spp..... | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | |
| <i>Betula lenta</i> | 40 | 4 | 25 | 5 | 7 | 3 | 26 | 3 | |
| <i>B. lutea</i> | 0 | 0 | 0 | 0 | 7 | 0 | 2 | 0 | |
| <i>Fagus grandifolia</i> | 60 | 12 | 100 | 18 | 21 | 3 | 77 | 16 | |
| <i>Fraxinus americana</i> | 47 | 5 | 57 | 11 | 14 | 0 | 49 | 5 | |
| <i>Hamamelis virginiana</i> | 7 | 0 | 0 | 0 | 0 | 0 | 12 | 1 | |
| <i>Magnolia acuminata</i> | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | |
| <i>Ostrya virginiana</i> | 27 | 2 | 50 | 4 | 43 | 2 | 49 | 4 | |
| <i>Pinus Strobus</i> | 0 | 0 | 0 | 0 | 7 | 0 | 5 | 0 | |
| <i>Populus grandidentata</i> | 7 | 0 | 0 | 0 | 0 | 0 | 5 | 9 | |
| <i>Prunus pensylvanica</i> | 7 | 2 | 13 | 0 | 0 | 0 | 26 | 4 | |
| <i>P. serotina</i> | 7 | 1 | 0 | 0 | 0 | 0 | 9 | 1 | |
| <i>Quercus alba</i> | 60 | 9 | 13 | 4 | 21 | 1 | 19 | 2 | |
| <i>Q. borealis</i> | 80 | 19 | 38 | 3 | 100 | 37 | 56 | 11 | |
| <i>Q. Prinus</i> | 14 | 2 | 0 | 0 | 57 | 18 | 12 | 0 | |
| <i>Tsuga canadensis</i> | 73 | 19 | 88 | 45 | 14 | 0 | 81 | 28 | |

TABLE 8. Summary of sample plot data for the shrub layer of vegetation at Smiley's Woods and Connecticut Hill, 1955 and 1956. Details as in Table 7.

| Smiley's Woods | | | | | | | | | |
|-----------------------------------|------------|----|------------|----|------------|----|------------|----|--|
| Number of plots | 1955 | | | | 1956 | | | | |
| | P.l. plots | | P.m. plots | | P.l. plots | | P.m. plots | | |
| | 9 | | 20 | | 9 | | 49 | | |
| | F. | C. | F. | C. | F. | C. | F. | C. | |
| <i>Acer nigrum</i> | 78 | 10 | 100 | 12 | 78 | 11 | 84 | 8 | |
| <i>A. pennsylvanicum</i> | 22 | 2 | 30 | 1 | 22 | 1 | 20 | 1 | |
| <i>Betula lutea</i> | 11 | 0 | 20 | 1 | 0 | 0 | 16 | 1 | |
| <i>Carpinus caroliniana</i> | 11 | 1 | 15 | 1 | 0 | 0 | 18 | 1 | |
| <i>Carya ovata</i> | 11 | 1 | 10 | 0 | 11 | 1 | 6 | 0 | |
| <i>Fagus grandifolia</i> | 100 | 14 | 80 | 9 | 78 | 7 | 88 | 9 | |
| <i>Fraxinus americana</i> | 0 | 0 | 35 | 1 | 0 | 0 | 20 | 1 | |
| <i>Hamamelis virginiana</i> | 0 | 0 | 50 | 6 | 11 | 1 | 25 | 2 | |
| <i>Magnolia acuminata</i> | 0 | 0 | 5 | 0 | 0 | 0 | 6 | 0 | |
| <i>Ostrya virginiana</i> | 22 | 1 | 45 | 1 | 22 | 1 | 27 | 1 | |
| <i>Prunus serotina</i> | 0 | 0 | 10 | 1 | 22 | 1 | 8 | 0 | |
| <i>Quercus borealis</i> | 0 | 0 | 20 | 1 | 0 | 0 | 10 | 0 | |
| <i>Tilia americana</i> | 0 | 0 | 25 | 1 | 11 | 0 | 14 | 0 | |
| <i>Tsuga canadensis</i> | 0 | 0 | 30 | 2 | 0 | 0 | 10 | 1 | |
| <i>Viburnum acerifolium</i> | 22 | 1 | 25 | 0 | 0 | 0 | 10 | 0 | |

| Connecticut Hill | | | | | | | | | |
|-----------------------------------|------------|----|------------|----|------------|----|------------|----|--|
| Number of plots | 1955 | | | | 1956 | | | | |
| | P.l. plots | | P.m. plots | | P.l. plots | | P.m. plots | | |
| | 15 | | 8 | | 14 | | 43 | | |
| | F. | C. | F. | C. | F. | C. | F. | C. | |
| <i>Acer nigrum</i> | 40 | 1 | 63 | 2 | 29 | 1 | 42 | 2 | |
| <i>A. pennsylvanicum</i> | 7 | 0 | 13 | 0 | 7 | 0 | 26 | 2 | |
| <i>A. rubrum</i> | 20 | 1 | 0 | 0 | 71 | 4 | 14 | 1 | |
| <i>Amelanchier</i> spp..... | 14 | 1 | 0 | 0 | 0 | 0 | 5 | 0 | |
| <i>Carpinus caroliniana</i> | 7 | 0 | 0 | 0 | 0 | 0 | 2 | 1 | |
| <i>Castanea dentata</i> | 0 | 0 | 0 | 0 | 43 | 2 | 2 | 0 | |
| <i>Fagus grandifolia</i> | 40 | 2 | 63 | 6 | 14 | 3 | 56 | 5 | |
| <i>Fraxinus americana</i> | 0 | 0 | 0 | 0 | 7 | 0 | 12 | 0 | |
| <i>Hamamelis virginiana</i> | 40 | 3 | 25 | 3 | 86 | 8 | 37 | 2 | |
| <i>Ostrya virginiana</i> | 53 | 2 | 38 | 3 | 14 | 1 | 33 | 2 | |
| <i>Pinus Strobus</i> | 0 | 0 | 0 | 0 | 14 | 1 | 0 | 0 | |
| <i>Prunus serotina</i> | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | |
| <i>Quercus borealis</i> | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | |
| <i>Tsuga canadensis</i> | 40 | 2 | 38 | 1 | 0 | 0 | 33 | 4 | |
| <i>Viburnum acerifolium</i> | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 | |

studies to investigate the nature of the vegetation in the home ranges of individuals of each species. Some of the trap stations in each area were not sampled because of lack of time. For each trapping period, sample plots at stations visited by mice of each kind were summarized for frequency of occurrence and average percentage of cover of species in the ground, shrub and tree layers of vegetation. These data are contained in Tables 7 through 11. Lists of plant species include only the more common ones of each study area. For shrubs and trees, only those species found on at least 5% of the sample plots of any one area are listed. The lists include about 75% of the species found. Species of the ground layer found on at least 15% of sample plots of any one area are listed;

the lists include about 25% of species found. Values have been rounded off to the nearest whole number. Many of the ground layer species had average percentage of cover values which were less than 0.5, and consequently appear as zero values.

The plant species which seem to show significant differences between *P. l. noveboracensis* and *P. m. gracilis* sample plots are mostly those species used in calculation of coefficients of interspecific association and are listed in Table 3.

In addition, the percentage of cover of all the vegetation in the ground layer was estimated at each trap station. Average for *P. l. noveboracensis* stations and for *P. m. gracilis* stations were calculated. For each trapping period, t-tests for statistical significance were run between these two groups. Table 12 summarizes the results.

The data concerning the occurrence of mor and mull humus on the study areas did not appear to exhibit any relationship to the distribution of mouse species.

Interspecific association.—In the studies of interspecific association between the forms of *Peromyscus* and species of plants, all trap stations for each trapping period were used in calculating coefficients of association, except those stations where mice of doubtful identity occurred. Therefore, this method sampled the vegetation of the area (in terms of the selected species) more thoroughly than did the sample plot method. Quantitative data were not obtained, however, mere presence or absence of a species being noted. Associations measured were between each species of mouse and each of the eight categories of vegetation shown in Table 3. Five of the eight categories were each comprised of a single typical plant species. The other three categories were each made up of a number of species, the presence of any one at a trap station counting for presence of the category. Associations between mouse species and plant categories were measured by using both variations of Cole's (1957) method. The method involving just two species has been described in the section dealing with interspecific relationships of *P. l. noveboracensis* and *P. m. gracilis*. This method was used to measure simply the association between each kind of mouse and each of the eight plant categories. These data are given in Table 13. The second variation involved measuring the association of a mouse species with a particular plant category, in the presence and absence of a second plant category. This has been termed the measurement of partial interspecific association (Cole 1957). These calculations were carried out for each species of *Peromyscus* and the eight plant categories. The data are not presented here because they agree substantially with the data of simple interspecific association and their length does not justify inclusion.

Associations were measured separately for the 1955 and 1956 trapping periods on each area. All of the trapping data were then combined, including

TABLE 9. Summary of sample plot data for the ground layer of vegetation at Smiley's Woods and Connecticut Hill, 1955 and 1956. Details as in Table 7.

| Smiley's Woods | | | | | | | | |
|---|------------|----|------------|----|------------|----|------------|----|
| Number of plots | 1955 | | | | 1956 | | | |
| | P.l. plots | | P.m. plots | | P.l. plots | | P.m. plots | |
| | 9 | | 20 | | 9 | | 49 | |
| | F. | C. | F. | C. | F. | C. | F. | C. |
| <i>Herbaceous angiosperms</i> | | | | | | | | |
| <i>Arisaema triphyllum</i> | 0 | 0 | 5 | 0 | 44 | 2 | 10 | 0 |
| <i>Aster</i> spp..... | 44 | 1 | 45 | 1 | 44 | 2 | 49 | 1 |
| <i>Carex</i> spp..... | 0 | 0 | 25 | 0 | 11 | 0 | 16 | 0 |
| <i>Epifagus virginiana</i> | 33 | 1 | 10 | 0 | 22 | 0 | 14 | 0 |
| <i>Epipactis helleborine</i> | 0 | 0 | 60 | 0 | 33 | 0 | 37 | 0 |
| <i>Gaultheria procumbens</i> | 11 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| <i>Grasses</i> | 0 | 0 | 20 | 1 | 22 | 1 | 16 | 0 |
| <i>Maianthemum canadense</i> | 44 | 1 | 30 | 1 | 11 | 1 | 33 | 1 |
| <i>Mitchella repens</i> | 0 | 0 | 15 | 0 | 0 | 0 | 10 | 0 |
| <i>Monotropa uniflora</i> | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| <i>Prenanthes</i> sp..... | 11 | 0 | 10 | 0 | 0 | 0 | 12 | 0 |
| <i>Solidago caesia</i> | 0 | 0 | 0 | 0 | 11 | 0 | 4 | 0 |
| <i>Trillium</i> sp..... | 0 | 0 | 25 | 1 | 11 | 0 | 25 | 0 |
| <i>Uvularia sessilifolia</i> | 11 | 0 | 20 | 0 | 0 | 0 | 25 | 0 |
| <i>Viola</i> spp..... | 11 | 0 | 35 | 1 | 22 | 1 | 22 | 1 |
| <i>Woody angiosperms</i> | | | | | | | | |
| <i>Acer nigrum</i> | 78 | 2 | 50 | 1 | 78 | 3 | 57 | 1 |
| <i>A. pennsylvanicum</i> | 22 | 0 | 15 | 0 | 33 | 1 | 34 | 1 |
| <i>A. rubrum</i> | 22 | 0 | 10 | 0 | 22 | 0 | 14 | 0 |
| <i>Amelanchier</i> spp..... | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Fagus grandifolia</i> | 56 | 1 | 20 | 0 | 67 | 1 | 33 | 1 |
| <i>Fraxinus americana</i> | 33 | 0 | 20 | 0 | 33 | 1 | 22 | 0 |
| <i>Hamamelis virginiana</i> | 0 | 0 | 10 | 0 | 0 | 0 | 2 | 0 |
| <i>Ostrya virginiana</i> | 22 | 0 | 5 | 0 | 22 | 0 | 20 | 0 |
| <i>Prunus</i> spp..... | 22 | 0 | 15 | 0 | 33 | 1 | 8 | 0 |
| <i>Quercus borealis</i> | 0 | 0 | 10 | 0 | 11 | 0 | 4 | 0 |
| <i>Tilia americana</i> | 11 | 0 | 15 | 0 | 11 | 0 | 10 | 0 |
| <i>Viburnum acerifolium</i> | 56 | 1 | 30 | 0 | 11 | 1 | 28 | 1 |
| <i>Miscellaneous</i> | | | | | | | | |
| <i>Dryopteris</i> spp..... | 0 | 0 | 60 | 2 | 0 | 0 | 30 | 2 |
| <i>Lycopodium</i> spp..... | 0 | 0 | 10 | 0 | 0 | 0 | 6 | 0 |
| <i>Polystichum acrostichoides</i> | 0 | 0 | 80 | 4 | 11 | 1 | 40 | 2 |

the snap-trapping data of 1957. Presence of a mouse at a trap station, in any trapping season, fulfilled the criterion for presence of the species at that trap station. These trapping data were used in calculating coefficients of interspecific association which are found in Table 13 under the heading "1955-57."

Water consumption experiment.—During the summer of 1955, the water consumption of 5 individuals of each species was measured for 40 days. The sex composition of each group was about the same, with a preponderance of males. Water was freely supplied by the use of drip tubes. The mice were weighed at the beginning and at the end of the observation period, and an average weight was obtained for each. For the *P. l. noveboracensis* group, the average amount of water consumed per gram of body weight per day was 0.43 cc. The comparable figure for the *P. m. gracilis* group was 0.42 cc. The average amount of water consumed by an individual per day was 7.6 cc for the *P. l. noveboracensis*

TABLE 9. (Continued)

| Connecticut Hill | | | | | | | | |
|---|------------|----|------------|----|------------|----|------------|----|
| Number of plots | 1955 | | | | 1956 | | | |
| | P.l. plots | | P.m. plots | | P.l. plots | | P.m. plots | |
| | 15 | | 8 | | 14 | | 43 | |
| | F. | C. | F. | C. | F. | C. | F. | C. |
| <i>Herbaceous angiosperms</i> | | | | | | | | |
| <i>Aster</i> spp..... | 40 | 1 | 13 | 0 | 86 | 3 | 16 | 0 |
| <i>Carex</i> spp..... | 27 | 2 | 0 | 0 | 50 | 6 | 16 | 1 |
| <i>Epifagus virginiana</i> | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| <i>Gaultheria procumbens</i> | 20 | 1 | 0 | 0 | 14 | 1 | 0 | 0 |
| <i>Grasses</i> | 0 | 0 | 0 | 0 | 36 | 2 | 9 | 0 |
| <i>Maianthemum canadense</i> | 33 | 1 | 0 | 0 | 57 | 2 | 9 | 0 |
| <i>Mitchella repens</i> | 33 | 1 | 25 | 1 | 0 | 0 | 37 | 1 |
| <i>Monotropa uniflora</i> | 13 | 0 | 13 | 0 | 14 | 0 | 14 | 0 |
| <i>Polygala paucifolia</i> | 27 | 1 | 0 | 0 | 21 | 0 | 5 | 0 |
| <i>Prenanthes</i> sp..... | 27 | 0 | 0 | 0 | 36 | 1 | 7 | 0 |
| <i>Solidago caesia</i> | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| <i>Trillium</i> sp..... | 7 | 0 | 0 | 0 | 0 | 0 | 2 | 0 |
| <i>Uvularia sessilifolia</i> | 47 | 1 | 38 | 1 | 50 | 2 | 37 | 1 |
| <i>Viola</i> spp..... | 13 | 0 | 0 | 0 | 43 | 2 | 21 | 0 |
| <i>Woody angiosperms</i> | | | | | | | | |
| <i>Acer nigrum</i> | 80 | 3 | 100 | 5 | 71 | 3 | 81 | 3 |
| <i>A. pennsylvanicum</i> | 13 | 0 | 0 | 0 | 0 | 0 | 21 | 1 |
| <i>A. rubrum</i> | 54 | 1 | 50 | 1 | 100 | 4 | 51 | 1 |
| <i>Amelanchier</i> spp..... | 67 | 2 | 13 | 0 | 79 | 3 | 33 | 1 |
| <i>Carpinus caroliniana</i> | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 |
| <i>Fagus grandifolia</i> | 40 | 1 | 75 | 2 | 14 | 1 | 51 | 2 |
| <i>Fraxinus americana</i> | 40 | 1 | 63 | 1 | 36 | 1 | 37 | 1 |
| <i>Hamamelis virginiana</i> | 33 | 2 | 13 | 1 | 71 | 3 | 21 | 1 |
| <i>Ostrya virginiana</i> | 73 | 6 | 88 | 4 | 21 | 1 | 70 | 4 |
| <i>Prunus</i> spp..... | 40 | 1 | 38 | 0 | 50 | 1 | 40 | 1 |
| <i>Quercus borealis</i> | 27 | 0 | 0 | 0 | 43 | 1 | 7 | 0 |
| <i>Q. Prinus</i> | 0 | 0 | 0 | 0 | 7 | 0 | 0 | 0 |
| <i>Rhododendron nudiflorum</i> | 13 | 1 | 0 | 0 | 36 | 2 | 5 | 0 |
| <i>Vaccinium angustifolium</i> | 27 | 1 | 0 | 0 | 71 | 4 | 9 | 0 |
| <i>Viburnum acerifolium</i> | 73 | 3 | 63 | 3 | 71 | 3 | 54 | 2 |
| <i>Miscellaneous</i> | | | | | | | | |
| <i>Dryopteris</i> spp..... | 0 | 0 | 0 | 0 | 0 | 0 | 9 | 0 |
| <i>Lycopodium</i> spp..... | 7 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| <i>Polystichum acrostichoides</i> | 0 | 0 | 13 | 1 | 7 | 0 | 7 | 1 |
| <i>Pteridium aquilinum</i> | 0 | 0 | 0 | 0 | 29 | 1 | 0 | 0 |

group, and 7.4 cc for the *P. m. gracilis* group. No statistically significant differences between groups were indicated by t-tests. The water consumption figures were somewhat higher than have been reported for these forms. Odum (1944) noted an average daily consumption of 2.6 cc for 5 *P. l. noveboracensis* and 1.8 cc for one *P. m. nubiterrae*. Lindeborg (1952) found that two groups of *P. l. noveboracensis*, with 20 individuals per group, consumed 2.54 cc and 2.46 cc per individual daily. The average daily consumption of individuals of *P. m. gracilis*, in three groups of 10 mice each, was 3.21, 1.71 and 2.72 cc. The greater amount of water consumed by mice in the present study may have been due to the experimental conditions. The mice were kept in wire mesh cages in an open shed. Summer-time temperatures and optimum conditions for air movement may have caused much evaporation from the animals. Some loss from the drip tubes also occurred through evaporation and handling.

TABLE 10. Summary of sample plot data for the tree and shrub layers of vegetation at Arnot Forest, 1955 and 1956. Details as in Table 7.

| Number of plots | Tree Layer | | | | | |
|------------------------------------|------------|----|------------|----|------------|----|
| | 1955 | | 1956 | | | |
| | P.L. plots | | P.L. plots | | P.m. plots | |
| | 24 | | 86 | | 26 | |
| | F. | C. | F. | C. | F. | C. |
| <i>Acer nigrum</i> | 25 | 2 | 73 | 27 | 92 | 43 |
| <i>A. rubrum</i> | 88 | 10 | 56 | 11 | 15 | 3 |
| <i>Amelanchier</i> spp..... | 21 | 1 | 7 | 0 | 4 | 0 |
| <i>Betula lenta</i> | 0 | 0 | 12 | 1 | 8 | 1 |
| <i>B. lutea</i> | 0 | 0 | 2 | 0 | 8 | 1 |
| <i>Carpinus caroliniana</i> | 4 | 0 | 4 | 1 | 4 | 0 |
| <i>Carya ovata</i> | 0 | 0 | 1 | 0 | 0 | 0 |
| <i>Fagus grandifolia</i> | 29 | 7 | 47 | 10 | 73 | 24 |
| <i>Fraxinus americana</i> | 8 | 0 | 42 | 4 | 42 | 4 |
| <i>Ostrya virginiana</i> | 4 | 0 | 11 | 1 | 15 | 1 |
| <i>Pinus strobus</i> | 58 | 6 | 17 | 2 | 0 | 0 |
| <i>Populus grandidentata</i> | 38 | 1 | 6 | 0 | 4 | 0 |
| <i>Prunus serotina</i> | 0 | 0 | 2 | 0 | 0 | 0 |
| <i>Quercus borealis</i> | 25 | 9 | 15 | 4 | 4 | 0 |
| <i>Q. prinus</i> | 79 | 40 | 38 | 15 | 0 | 0 |
| <i>Tilia americana</i> | 38 | 1 | 23 | 4 | 27 | 4 |
| <i>Tsuga canadensis</i> | 50 | 11 | 48 | 12 | 42 | 8 |

| Number of plots | Shrub Layer | | | | | |
|-----------------------------------|-------------|----|------------|----|------------|----|
| | 1955 | | 1956 | | | |
| | P.L. plots | | P.L. plots | | P.m. plots | |
| | 24 | | 86 | | 26 | |
| | F. | C. | F. | C. | F. | C. |
| <i>Acer nigrum</i> | 17 | 1 | 42 | 4 | 46 | 3 |
| <i>A. pennsylvanicum</i> | 0 | 0 | 12 | 0 | 39 | 2 |
| <i>A. rubrum</i> | 63 | 3 | 21 | 1 | 0 | 0 |
| <i>Amelanchier</i> spp..... | 63 | 3 | 19 | 1 | 0 | 0 |
| <i>Carpinus caroliniana</i> | 8 | 0 | 12 | 46 | 0 | 0 |
| <i>Castanea dentata</i> | 13 | 0 | 4 | 0 | 0 | 0 |
| <i>Fagus grandifolia</i> | 46 | 3 | 40 | 3 | 58 | 4 |
| <i>Fraxinus americana</i> | 4 | 0 | 7 | 0 | 0 | 0 |
| <i>Hamamelis virginiana</i> | 8 | 0 | 13 | 1 | 8 | 0 |
| <i>Ostrya virginiana</i> | 4 | 0 | 17 | 1 | 4 | 0 |
| <i>Pinus strobus</i> | 41 | 4 | 13 | 1 | 0 | 0 |
| <i>Prunus serotina</i> | 4 | 0 | 1 | 0 | 0 | 0 |
| <i>Quercus borealis</i> | 46 | 2 | 13 | 1 | 0 | 0 |
| <i>Q. prinus</i> | 58 | 5 | 16 | 2 | 0 | 0 |
| <i>Tilia americana</i> | 0 | 0 | 4 | 0 | 4 | 0 |
| <i>Tsuga canadensis</i> | 29 | 3 | 48 | 7 | 50 | 10 |

DISCUSSION

ECOLOGICAL RELATIONSHIPS OF PEROMYSCUS SPECIES TO VEGETATION

The measurements of interspecific association (Table 13) appear to indicate an affinity of *Peromyscus maniculatus gracilis* for habitats occupied by plants listed in Table 3 as typical for the Hemlock-White Pine-Northern Hardwoods Forest region. Individuals of *P. m. gracilis* also appeared to avoid sites of plants typical of the Oak-Chestnut Forest region. Although *P. leucopus noveboracensis* did not exhibit so marked a difference in its choice of habitat, it showed an inverse relationship to *P. m. gracilis* respecting the two habitat groups of plants.

TABLE 11. Summary of sample plot data for the ground layer of vegetation at Arnot Forest, 1955 and 1956. Details as in Table 7.

| Number of plots | 1955 | | 1956 | | | |
|---|------------|----|------------|----|------------|----|
| | P.L. plots | | P.L. plots | | P.m. plots | |
| | 24 | | 86 | | 26 | |
| | F. | C. | F. | C. | F. | C. |
| | F. | C. | F. | C. | F. | C. |
| <i>Herbaceous angiosperms</i> | | | | | | |
| <i>Arisaema triphyllum</i> | 0 | 0 | 13 | 0 | 15 | 0 |
| <i>Aster</i> spp..... | 38 | 1 | 43 | 2 | 35 | 1 |
| <i>Carex</i> spp..... | 46 | 2 | 43 | 2 | 15 | 1 |
| <i>Epifagus virginiana</i> | 4 | 0 | 6 | 0 | 12 | 0 |
| <i>Epipactis helleborine</i> | 4 | 0 | 12 | 0 | 19 | 1 |
| <i>Gaultheria procumbens</i> | 75 | 4 | 29 | 1 | 0 | 0 |
| Grasses..... | 21 | 1 | 19 | 1 | 4 | 0 |
| <i>Maianthemum canadense</i> | 21 | 1 | 30 | 1 | 42 | 2 |
| <i>Mitchella repens</i> | 0 | 0 | 5 | 0 | 8 | 0 |
| <i>Monotropa uniflora</i> | 0 | 0 | 5 | 0 | 4 | 0 |
| <i>Polygala paucifolia</i> | 21 | 0 | 12 | 0 | 0 | 0 |
| <i>Prenanthes</i> sp..... | 0 | 0 | 15 | 0 | 8 | 0 |
| <i>Solidago caesia</i> | 21 | 1 | 28 | 1 | 12 | 0 |
| <i>Trillium</i> sp..... | 8 | 0 | 6 | 0 | 4 | 0 |
| <i>Uvularia sessilifolia</i> | 21 | 0 | 28 | 0 | 15 | 0 |
| <i>Viola</i> spp..... | 21 | 0 | 38 | 1 | 46 | 1 |
| <i>Woody angiosperms</i> | | | | | | |
| <i>Acer nigrum</i> | 21 | 0 | 59 | 7 | 85 | 15 |
| <i>A. pennsylvanicum</i> | 0 | 0 | 14 | 0 | 27 | 1 |
| <i>A. rubrum</i> | 41 | 1 | 62 | 2 | 39 | 1 |
| <i>Amelanchier</i> spp..... | 71 | 3 | 37 | 1 | 15 | 0 |
| <i>Carpinus caroliniana</i> | 13 | 0 | 21 | 1 | 12 | 0 |
| <i>Fagus grandifolia</i> | 38 | 1 | 51 | 2 | 58 | 3 |
| <i>Fraxinus americana</i> | 8 | 0 | 42 | 1 | 50 | 1 |
| <i>Hamamelis virginiana</i> | 8 | 0 | 11 | 0 | 0 | 0 |
| <i>Ostrya virginiana</i> | 33 | 1 | 54 | 2 | 31 | 0 |
| <i>Prunus</i> spp..... | 4 | 0 | 4 | 0 | 8 | 0 |
| <i>Quercus borealis</i> | 41 | 1 | 27 | 1 | 19 | 0 |
| <i>Q. prinus</i> | 75 | 5 | 31 | 2 | 0 | 0 |
| <i>Rhododendron nudiflorum</i> | 17 | 1 | 5 | 0 | 0 | 0 |
| <i>Tilia americana</i> | 8 | 0 | 14 | 0 | 19 | 0 |
| <i>Vaccinium angustifolium</i> | 54 | 7 | 17 | 2 | 0 | 0 |
| <i>Viburnum acerifolium</i> | 17 | 1 | 12 | 0 | 15 | 0 |
| <i>Miscellaneous</i> | | | | | | |
| <i>Dryopteris</i> spp..... | 4 | 0 | 42 | 2 | 65 | 4 |
| <i>Lycopodium</i> spp..... | 4 | 0 | 11 | 1 | 19 | 1 |
| <i>Polystichum acrostichoides</i> | 4 | 0 | 20 | 1 | 15 | 0 |
| <i>Pteridium aquilinum</i> | 38 | 2 | 12 | 1 | 0 | 0 |

TABLE 12. Average percentage of cover of the ground layer of vegetation at *P. l. noveboracensis* (P.L.) and *P. m. gracilis* (P.m.) stations on three study areas, 1955 and 1956. Asterisks indicate statistically significant differences at the 5% level (*) and 1% level (**) between averages of P.L. and P.m. stations.

| | 1955 | | 1956 | |
|-----------------------|------|------|------|------|
| | P.L. | P.m. | P.L. | P.m. |
| Smiley's Woods..... | 7 | * | 16 | |
| Connecticut Hill..... | 19 | | 24 | * |
| Arnot Forest..... | 38 | — | 36 | 36 |

It was found most frequently at places where plants typical of the Oak-Chestnut region occurred and

TABLE 13. Coefficients of association between *P. l. noveboracensis* (P.l.) or *P. m. gracilis* (P.m) and plant groups listed in Table 3. At Arnot Forest, 1955, *P. m. gracilis* was not taken. Dash-marks for other items indicate that the plant species were not present at trap stations on the area. At Connecticut Hill, 1955, the association with P.D.D.D. was not measurable because of too few stations at which plant species represented by P.D.D.D. were present. Asterisks indicate statistical significance at the 5% level (*) and at the 1% level (**).

| | Smiley's Woods | | | Connecticut Hill | | | Arnot Forest | | |
|-------------------|----------------|-------|---------|------------------|---------|---------|--------------|---------|---------|
| | 1955 | 1956 | 1955-57 | 1955 | 1956 | 1955-57 | 1955 | 1956 | 1955-57 |
| P.l.-T.B.A..... | -.44** | -.35 | -.31* | -.11 | -.63** | -.24** | -.28 | -.33* | -.34* |
| P.m.-T.B.A..... | +.73** | -.05 | +.14 | +.55 | +.53** | +.57** | | -.05 | +.02 |
| P.l.-P.D.D.D..... | -.88** | -.41 | -.66** | | -.23 | -.57 | -.36 | -.40** | -.51** |
| P.m.-P.D.D.D..... | +.33* | -.10 | -.11 | | +.23 | +.18 | | +.58** | +.54** |
| P.l.-F.g..... | +1.00** | +.13 | +.80* | 0.00 | -.54* | -.01 | +.03 | -.29* | -.30* |
| P.m.-F.g..... | -.51* | +.17 | -.19 | +1.00** | +.42** | +.53** | | +.30 | +.36* |
| P.l.-A.n..... | +.63 | +1.00 | +.59 | -.02 | -.15 | -.08 | -.25 | -.34 | -.48* |
| P.m.-A.n..... | -.50* | +.23 | -.53 | -.03 | +.04 | -.01 | | +.70* | +.73* |
| P.l.-Q.a..... | | | | +.35* | -.16 | +.09 | | | |
| P.m.-Q.a..... | | | | -.76* | -.40** | -.45** | | | |
| P.l.-Q.b..... | +.45** | -.48 | +.23 | +.37 | +1.00** | +.53* | -.16 | +.81* | +.80* |
| P.m.-Q.b..... | -.40 | +.01 | -.06 | -.33 | -.34** | -.39** | | -.65 | -.37 |
| P.l.-R.V.G.P..... | | | | +.07 | +.51** | +.18 | +.40** | +.90** | +1.00** |
| P.m.-R.V.G.P..... | | | | -1.00* | -.68** | -.66** | | -1.00** | -1.00** |
| P.l.-Q.P..... | | | | -.33 | +.39** | +.05 | +.39 | +.60** | +.72** |
| P.m.-Q.P..... | | | | -.09 | -.51** | -.38** | | -1.00** | -1.00** |

avoided sites of plants of the Hemlock-White Pine-Northern Hardwoods region. Considering only the measurements of simple association between a species of *Peromyscus* and a plant category, there are 57 values in Table 13 which show statistically significant positive or negative coefficients. Fifty-three of these agree with the situations outlined above and four deviate. The 4 deviations all occurred in Smiley's Woods and involved *Fagus grandifolia* (beech) or *Acer nigrum* (sugar maple) trees. These species were widely distributed on this study area and, together with *Tsuga canadensis* (hemlock), were the dominant tree species. Of the 126 stations used during the study, *Acer nigrum* was present at 112, *Fagus grandifolia* at 105 and *Tsuga canadensis* at 47. Species typical of the Oak-Chestnut region were very poorly represented in Smiley's Woods. *Quercus borealis* (red oak) was present at 19 stations and *Gaultheria procumbens* (winterberry) at 4. No other species of this group were recorded from the 126 stations at which observations were made.

In Smiley's Woods, *Fagus grandifolia* and *Acer nigrum* were distributed evenly over the trapping grid except in the area of stations 9-11 on lines G-L. They were much less abundant here and were replaced by *Tsuga canadensis*, *Betula lutea* (yellow birch) and *Acer pennsylvanicum* (striped maple), which had their center of abundance in this area. Fig. 1 indicates that in 1955, *P. m. gracilis* was generally distributed in this area, while *P. l. noveboracensis* was found in the western part of the trapping grid where *Acer*

nigrum and *Fagus grandifolia* were abundant. These distributional facts are responsible for the $-.50^*$ coefficient of association for *P. m. gracilis* and *Acer nigrum*, the $-.51^*$ coefficient for *P. m. gracilis* and *Fagus grandifolia*, and the $+1.00^{**}$ coefficient for *P. l. noveboracensis* and *Fagus grandifolia*. Possible causes of this distribution will be discussed later.

In general, the sample plot data (Table 7-11) support and supplement those of measurements of association. They are particularly informative where the coefficients of simple association are not statistically significant. All of the plant species used in the measurements of association are present in the sample plot data. Other conspicuous plant species are included. The quantitative aspects of the data also aid in giving a more complete description of the habitat at *P. l. noveboracensis* and *P. m. gracilis* stations.

CLASSIFICATION OF WOODLAND COMMUNITIES

To establish the study areas within existing biogeographic schemes, a short summary is in order. All three areas are located near the northern edge of the Glaciated Allegheny Plateau (Fenneman 1938). They fall within Merriam's (1894) Transition life zone, Dice's (1943) Canadian biotic province and the Deciduous Forest biome of Clements and Shelford (Shelford 1945). The biome system is based on the climax formations of vegetation outlined by Weaver & Clements (1938). The study areas lie within the Maple-Beech association of their Deciduous Forest formation. According to a modification of the biome

system proposed by Kendeigh (1954), who used the term biociation to designate a climax biotic community of plants and animals, the study areas are within the ecotone (transitional area) between the Boreal Forest and Deciduous Forest biociations. On the basis of Bray's (1930) classification of the vegetational zones of New York, which recognizes six zones characterized by the combinations of dominant plant species present, the study areas are within Zone C (Allegheny-Transition), which is characterized by dominance of *Acer nigrum*, *Fagus grandifolia*, *Betula lutea*, *Tsuga canadensis* and *Pinus Strobus* (white pine). They also belong to the Hemlock-White Pine-Northern Hardwoods region of Braun (1950), and more precisely, within the Allegheny section of the Northern Appalachian Highland division of that region. *Fagus grandifolia*, *Tsuga canadensis* and *Acer nigrum* are the dominant trees of the climax forest of this area. Tree species which are considered part of the developmental stages of vegetation are *Castanea dentata* (chestnut), *Quercus borealis*, *Q. alba* (white oak), *Fraxinus americana* (white ash), *Acer rubrum* (red maple) and *Prunus* (cherry). The oaks are also dominant climax species in major forest regions to the south, the Mixed Mesophytic Forest region and the Oak-Chestnut Forest region (Braun 1950).

Hills (1952) has indicated the tree associations which occur on various sites in southern Ontario. (The modified terminology used here follows Odum 1953, p. 197.) The climatic climax association is maple-beech, occurring in habitats of normal microclimate over moist soil. Habitats of warmer microclimate over dry soil support an oak-chestnut edaphic climax association. Habitats of colder microclimate over dry soil support a hemlock-yellow birch edaphic climax association. These relationships presumably are valid for the study areas, since central New York and southern Ontario are climatically similar, and Braun's Hemlock-White Pine-Northern Hardwoods Forest region covers parts of both areas.

The climax plants of the Oak-Chestnut Forest region may form a physiographic climax vegetation in the Hemlock-White Pine-Northern Hardwoods region on areas of steep, south or west-facing slopes, which are xeric in nature due to high insolation and excessive drainage. This vegetation perpetuates itself so long as the physiographic conditions remain the same. A part of the Arnot Forest study area answers this description. The area of stations 17 through 20, on lines H through K, was situated on a steep, southwest-facing slope. The vegetation was characteristic of the drier slopes of the Oak-Chestnut Forest region (Braun 1950). Species abundant in the tree layer were *Quercus Prinus*, *Q. borealis* and *Pinus Strobus*. These species were also abundant in the shrub layer, as were *Acer rubrum* and *Amelanchier* sp. In the ground layer, *Quercus Prinus*, *Q. borealis*, *Amelanchier* sp., *Vaccinium angustifolium*, *Gaultheria procumbens*, *Epigaea repens*

and *Pteridium aquilinum* were abundant. The predominance of *Quercus Prinus* in the tree layer, and the abundance of ericaceous plants in the ground layer, are the outstanding features of this type of vegetation. That it was not a temporary developmental stage in plant succession on the area was indicated by the abundance of *Q. Prinus* in the ground and shrub layers. The rest of the Arnot Forest study area was much more mesic, and *Acer nigrum* and *Fagus grandifolia* (species of the climatic climax vegetation) were dominant. It is noteworthy that only *P. l. noveboracensis* was taken in the *Quercus Prinus* physiographic climax area and that *P. m. gracilis* was not. *P. m. gracilis* was trapped only in areas of climatic climax vegetation.

The Connecticut Hill study area was an example of the transition of vegetation from a more open, up-slope habitat, supporting what appeared to be a developmental stage of vegetation, down the slope to a more shaded habitat with vegetation of a more climatic aspect. *Quercus Prinus* was present only at the top of the slope. *Q. borealis* and *Q. alba* were generally distributed, but were more abundant on the upper parts of the slope. *Fagus grandifolia*, *Acer nigrum* and *Tsuga canadensis* were not abundant at the top of the slope, but became so farther down the slope. The presence of *Quercus Prinus* and its xeric associates did not indicate, in this case, a physiographic climax as at the Arnot Forest area. The slope was not dry enough due to its gentle pitch and east exposure. Indication that this vegetation was not perpetuating itself is provided by data from the sample plot studies. None of the sample plots contained *Q. Prinus* in the shrub layer, and only one seedling was found in the ground layer. Presence of *Q. Prinus* and its associates is explained by the openness of the woodland to the west of the trapping grid. It had once been a cultivated field, and the trees present on the area were not yet large enough to form a closed-canopy forest. The *Q. Prinus* was probably established at a time when this area was more exposed to sun and wind because of the open field. The large number of *Q. borealis* and *Q. alba* on the Connecticut Hill area may be attributed in part to disturbance of the vegetation. Lumbering had undoubtedly been a part of the history of the area and some cutting of trees had been done several decades before as part of a game management program. Indication that climax vegetation would eventually be dominant on the area is provided by the sample plot studies. *Q. alba* was absent from the shrub and ground layers. *Q. borealis* was poorly represented in the ground layer and only a few shrubs of this species were found.

In comparing the 1956 trapping data for Connecticut Hill (Fig. 5) with the distribution of the six dominant tree species, it may be seen that *P. l. noveboracensis* occurred in the upper slope portion of the area. Here the oaks were abundant (particularly *Q. Prinus*) and *Fagus grandifolia*, *Acer ni-*

TABLE 14. Coefficients of simple and partial association between each species of *Peromyscus* and *Tsuga canadensis*. Asterisks indicate statistical significance at the 5% level (*) and 1% level (**). R.V.G.P. denotes a group of plants composed of *Rhododendron nudiflorum*, *Vaccinium angustifolium*, *Gaultheria procumbens*, and *Pteridium aquilinum*.

| | Smiley's Woods | | Connecticut Hill | | Arnot Forest | |
|-------------------------|----------------|------|------------------|--------|--------------|------|
| | 1955 | 1956 | 1955 | 1956 | 1955 | 1956 |
| P.l. Tsuga..... | -1.00** | -.67 | -.11 | -.72** | -.28 | -.07 |
| P.m. Tsuga..... | +.69** | +.16 | +.55 | +.38** | — | -.11 |
| P.l. Tsuga+R.V.G.P..... | — | — | — | -.46* | — | — |
| P.l. Tsuga-R.V.G.P..... | — | — | — | -1.00 | — | — |
| P.m. Tsuga+R.V.G.P.... | — | — | — | +.07 | — | — |
| P.m. Tsuga-R.V.G.P.... | — | — | — | +.54** | — | — |

grum and especially *Tsuga canadensis* were infrequent. *P. m. gracilis* was distributed generally over the lower portion of the slope, where *Q. Prinus* was infrequent or absent and *Fagus grandifolia*, *Acer nigrum* and *Tsuga canadensis* were abundant. Coefficients of association in Tables 13 and 14 consistently bear out these distributional relationships.

As has already been pointed out, the species composition of the tree layer in Smiley's Woods was typical of the climatic climax vegetation, except for the easternmost part of the area. At stations 9 through about 12 in each line, *Tsuga canadensis*, *Betula lutea* and *Acer pennsylvanicum* were generally distributed and largely replaced *Fagus grandifolia* and *Acer nigrum*. According to Hills (1952), a hemlock-yellow birch association constitutes an edaphic climax occurring on drier than normal soils with a colder than normal microclimate. *Acer pennsylvanicum* is a species of cool woods according to Fernald (1950). It was found in the same general habitats as *Tsuga canadensis* and *Betula lutea*. This area may be considered an edaphic (or physiographic) climax area in the *Fagus grandifolia*-*Acer nigrum* woodland of Smiley's Woods. It is interesting that, in 1955 and 1956, *P. m. gracilis* was most abundant in this area (Figs. 1 and 4). This may indicate an affinity of *P. m. gracilis* for such cooler areas of edaphic climax vegetation.

The general distribution of *P. l. noveboracensis* in the western part of the study area is strongly attributed to the presence of forest-edge and open field about 90 m west of the trapping grid. This factor will be discussed later in the section, "Population pressure and interspecific antagonism."

HABITAT SELECTION IN RELATION TO PSYCHOLOGICAL FACTORS

The observations of many workers have established the types of habitat in which these animals are usually found. *P. l. noveboracensis* occupies a wider range of vegetation life forms than does *P. m. gracilis*. It is frequently found in brushy fields,

fence rows and even in open fields far from woodland, in which it is usually most abundant. Trapping studies of *P. m. gracilis* have given the impression that it is restricted to mature woodland. Some exceptions have been reported. Manville (1949), working in northern Michigan, collected *P. m. gracilis* in and about buildings, in meadows and pasture lands, and one individual from a leather-leaf bog. Harper & Harper (1929) found *P. m. gracilis* living in the alpine zone of three Adirondack mountains. Barbehenn & New (1957) reported *P. m. gracilis* living in old fields near woodland in central New York. Dice & Sherman (1922) trapped it in shrubby areas in Michigan. Harris (1952) found it in young forest plantations where the trees were only a few feet tall. In some of these instances, population pressure may have been the cause of an emigration of mice from overcrowded forest habitats, which were presumably the preferred ones.

Various workers have investigated the problem of habitat selection in vertebrates. Shelford (1913) found that invertebrates and amphibians of moist, terrestrial habitats exhibited a marked avoidance of air of high evaporating power. Lack (1933) found that the height of Scots pines in plantations determined the kinds of birds nesting in the area. He believed that the birds selected these habitats on the basis of their conspicuous features, and that this selection was based on the psychological characteristics of the species. The biological advantage of such a mechanism would be to cause individuals to seek a suitable habitat for successful nesting. Kendeigh (1945) found that birds sought particular nesting sites in a habitat, and that these were characteristic for each species; in some species there was a selection of coniferous trees (*Tsuga canadensis*), and an avoidance of deciduous trees, for nesting. Kendeigh believed that the appearance of the two types of foliage provided the basis for selection, rather than microclimate or food supply associated with each kind of tree. Dice (1922) and Johnson (1926) experimented with *P. l. noveboracensis* and *P. maniculatus bairdii* (prairie deer mouse) in an effort to discover the factors that caused the former to inhabit forests, and the latter prairie; neither could find any differences between these animals in food, water, temperature or humidity requirements. They concluded that individuals of each form reacted instinctively toward the whole prairie or forest environment and its stimuli, rather than to any one factor present. Harris (1952) measured selection between two artificial habitats by two subspecies of *P. maniculatus*; *P. m. bairdii* selected a habitat simulating prairie, and *P. m. gracilis* selected a habitat simulating forest. He concluded that the objects in these artificial habitats (tree trunks in the forest habitat and Manila folders cut to resemble tufts of

grass in the prairie habitat) served as cues to which the individuals reacted in selecting a habitat.

Since the two forms in this study are essentially forest-dwellers, there is little concern with selection on the basis of gross differences in habitat, as with *P. m. bairdii* and *P. m. gracilis*. Whether there were finer degrees of perception and selection of habitat on the basis of tree density or ground cover density may be considered. Data for the estimation of the percentage of cover provided by the ground layer are recorded in Table 12. This measure also gives some indication of the amount of light reaching the lower vegetation, and therefore of the completeness of the tree canopy. In these two years at Connecticut Hill, the average amount of ground cover at *P. m. gracilis* stations was about one-half that at *P. l. noveboracensis* stations. A t-test showed this difference in 1956 to be statistically significant at the 5% level. At Smiley's Woods the results were contradictory. In 1956, *P. m. gracilis* stations had much less ground cover than *P. l. noveboracensis* stations, but in 1955 this situation was reversed. The higher average for *P. m. gracilis* stations was influenced by stations near the stream and trail at the east edge of the study area. These had an open tree canopy and consequently a more complete ground cover. At the Arnot Forest, 1956, *P. m. gracilis* stations had a high amount of ground cover, as did the *P. l. noveboracensis* stations. It is concluded that the amount of ground cover did not influence the distribution of these animals on the areas studied. The general tendency for *P. m. gracilis* stations to have a lower percentage of ground cover may be correlated with the climax type of vegetation and the restricted exposure of the areas these mice occupied. With one exception (Smiley's Woods, 1955), *P. l. noveboracensis* stations had high amounts of ground cover. This is correlated with the developmental stages of vegetation and the greater exposure of areas occupied by *P. l. noveboracensis*.

A factor which may have an influence on the distribution of mice is the amount of illumination reaching the forest floor at night, when these animals are active. Blair (1943) experimented with the effects of various light intensities on the activity of *P. maniculatus blandus*, a desert-dwelling deer mouse. He found that the mice were most active in total darkness. At light intensities equivalent to those of a clear, moonless night, the mice were still very active, but at about one-half the intensity of full moonlight, activity was significantly less. No comparable studies have been carried out on the forms concerned in this study. It is possible that density of the forest canopy, and also of the ground vegetation, would have a differential effect on habitat selection by mice of the two species, if they responded in activity to different thresholds of illumination.

The question may be raised as to whether there was any selection of habitat by these animals on the

basis of deciduous versus coniferous trees. The literature reviewed often indicated that *P. m. gracilis* was found in coniferous woods and *P. l. noveboracensis* in deciduous woods. The data from this study tend to support these observations (Table 14). At Smiley's Woods, 1955, and at Connecticut Hill, 1956, there was negative association between *P. l. noveboracensis* and *Tsuga canadensis*, and positive association between *P. m. gracilis* and *Tsuga canadensis*. These coefficients were statistically significant at the 1% level. None of the other coefficients was statistically significant, but almost all of them followed the same trend. Small numbers of both mice on the Connecticut Hill area in 1955 were partly responsible for the lack of statistical significance. The general distribution of *P. m. gracilis* on the Smiley's Woods study area in 1956 caused the measurement of association to indicate that the distribution of this species with respect to *Tsuga canadensis* was not significantly different from randomness. Small numbers of *P. l. noveboracensis* at Smiley's Woods in 1956 were responsible for lack of statistical significance of the coefficient of association between this mouse and *Tsuga canadensis*.

The contrasting coefficients of association between *Tsuga canadensis* and each of the species of mouse do not necessarily imply that the mice were attracted or repelled by *Tsuga canadensis* trees as such. This species may tend to grow in areas which the animals find favorable or unfavorable for other reasons. Some indication of this is provided by coefficients of partial association for each form of *Peromyscus* and *Tsuga canadensis*, in the presence and absence of *Rhododendron nudiflorum* (azalea), *Vaccinium angustifolium* (blueberry), *Pteridium aquilinum* (bracken fern) or *Gaultheria procumbens*. This group of four plants is abbreviated R.V.G.P. Data for these measurements at Connecticut Hill, 1956, are in Table 14. In each case, the absence of R.V.G.P. caused a larger coefficient of partial association (positive or negative) than simple association between each species of *Peromyscus* and *Tsuga canadensis*. Conversely, the presence of R.V.G.P. provides smaller coefficients of partial association between each kind of mouse and *Tsuga canadensis*, than do the measurements of simple association. The coefficient for *P. m. gracilis* and *Tsuga canadensis* in the presence of R.V.G.P. is +.07, while in the absence of R.V.G.P. it is +.54. The difference is statistically significant at the 1% level. This may indicate that conditions at the surface of the ground have a strong effect on the distribution of *P. m. gracilis*, and that this animal tends to avoid conditions which are favorable to the plant species represented by R.V.G.P. Conversely, *P. l. noveboracensis* appears to be attracted by conditions favorable to these plant species. This is indicated by its consistent positive association with R.V.G.P. (Table 13), and by the -1.00 coefficient of partial association of *P. l. noveboracensis* with *Tsuga cana-*

densis in the absence of R.V.G.P., which changes to -.46 in the presence of R.V.G.P. This difference is statistically significant at the 5% level.

It appears probable that the mice do not perceive and react to *Tsuga canadensis* on the basis of foliage as in the case of bird species studied by Kendeigh (1945). In fact, there does not seem to be any basis for concluding that the habitat differences between *P. m. gracilis* and *P. l. noveboracensis* reported in the literature and exhibited in this study have their basis in a psychological selection of habitat.

HABITAT SELECTION ON THE BASIS OF PHYSIOLOGICAL FACTORS

From the food habit studies of Hamilton (1941) and Cogshall (1928), it appears that *P. m. gracilis* and *P. l. noveboracensis* are alike in their food preferences. A possible factor in the positive association of *P. m. gracilis* with *Tsuga canadensis* may be a preference for its seeds or leaves as food. An indication that food supplied by this plant was not a basis for habitat selection by the two kinds of mice was provided by Cogshall (1928). She found that *P. l. noveboracensis* and *P. m. gracilis* were very similar in their readiness to eat spruce seeds. Extrapolating this information to another conifer, it seems reasonable to expect that there would not be any difference between the species in their preference for *Tsuga canadensis* seeds.

Some experimental work has been conducted on the water requirements of *P. l. noveboracensis* and *P. m. gracilis*. Lindeborg (1952) found that both species were similar in their reaction to a limited daily amount of water. Neither could survive on a ration of 0.2 cc per day, and at 0.4 cc individuals of both forms lost weight. *P. m. gracilis* individuals lost less weight than *P. l. noveboracensis* individuals. This may indicate a slightly smaller water requirement for *P. m. gracilis*. The observations on voluntary water consumption in this study and by Lindeborg (1952) indicated no difference between the species. It seems probable that the water economy of the two forms is similar in the wild. No experiments have been done to compare them with respect to humidity selection. A differential response to humidity at the soil surface, or to the amount of moisture in the soil, may be a factor in the local distribution of these mice. The experimental indications of similar water economy in the two forms make it probable that this is not so.

Various workers have experimented with *P. l. noveboracensis* and *P. m. gracilis* with respect to their reactions to low temperatures. No studies have been done to compare the two forms regarding temperature selection at normal summertime temperatures. Stinson & Fisher (1953) found that *P. maniculatus bairdii* selected temperatures between 20°C and 30°C. Observations on 4 *P. l. noveboracensis* in a different apparatus indicated selection of temperatures from 21°C to 26°C. There is

no experimental information to indicate whether there may be selection of habitat by *P. m. gracilis* and *P. l. noveboracensis* on the basis of a differential response to soil temperature. Soil surface temperatures were probably lower in the areas in which vegetation typical of the Hemlock-White Pine-Northern Hardwoods Forest region was dominant than temperatures in the adjacent areas of developmental vegetation typical of the Oak-Chestnut Forest region. Spaeth & Diebold (1938) studied soil temperatures under various kinds of vegetation at the Arnot Forest. They recognized a chestnut-oak type which occurred on south and west slopes. It was composed of "a pure, open, scrubby overstory of chestnut oak, with an irregularly developed understorey of aspen. . . ." A sugar maple-beech-yellow birch type occurred on north and east slopes and on broad hilltops. It contained very little *Betula lutea*, and there were varying amounts of *Tilia americana* (basswood), *Fraxinus americana* and *Tsuga canadensis*. A hemlock type was recognized as consisting of small areas within the preceding type. The aspen-birch type consisted of *Populus grandidentata* (large-toothed aspen), *P. tremuloides* (trembling aspen) and *Betula lenta* (black birch). It occurred on burned areas which formerly supported the sugar maple-beech-yellow birch type. At a depth of 2.5 cm, the average maximum soil temperature for mid-May to late June in both sugar maple-beech-yellow birch and aspen-birch types was 15.6°C (60°F.) and in the chestnut-oak type was 18.9°C. For the same types, the early July and mid-August temperatures were 20.0°C and 23.9°C, respectively. Soil temperatures measured for one year in a mature stand of hemlock were found to be very similar to those of nearby stations in the sugar maple-beech-yellow birch type. It was found that altitudinal differences of 92-214 m had little effect on soil temperatures, as type of cover and exposure obscured any differences due to altitude.

Air drainage may have been a factor in parts of some areas, but the study areas were generally on slopes which should have afforded good air drainage and prevented the accumulation of cold air in depressions. The funneling of cool air from higher areas into the narrow valleys on some of the study areas, as Smiley's Woods and Arnot Forest, may have caused colder microclimates in these places.

Soil temperatures were not measured in this study, and it is not known whether the nature or magnitude of temperature differences between *P. l. noveboracensis* and *P. m. gracilis* habitats was a factor in the observed distribution of the two animals. The 3.3°C and 3.9°C differences that Spaeth & Diebold (1938) found between sites with vegetation typical of the Oak-Chestnut Forest region, and sites with vegetation typical of the Hemlock-White Pine-Northern Hardwoods Forest region, suggest that *P. l. noveboracensis* habitats and *P. m. gracilis* habitats may have had significantly different soil tem-

peratures. The 21°C-26°C range of temperatures selected by 4 *P. l. noveboracensis* individuals (Stinson & Fisher 1953) appears to be narrow enough for differences in soil temperatures between warm and cool habitats to have had a differential effect on habitat selection by individuals of the two forms. That a difference in temperature preference may exist between these animals during the breeding season has yet to be determined experimentally.

Soil moisture and temperature are usually correlated to some degree in that moist soils are cooler than dry soils. Insolation on a soil surface will heat it, and will also cause it to become drier in the process. Moist soils warm up more slowly than dry soils. Evaporation of water from a soil serves to cool it. This interrelationship between soil moisture and temperature makes it difficult to separate the effects of one from the other in determining which may have had the greater effect on the local distribution of mice.

The experimental evidence of Lindeborg (1952), that *P. l. noveboracensis* and *P. m. gracilis* have the same water requirements, may indicate that soil moisture was not a differentiating factor in habitat selection by the mice. The altitudinal distribution of the two forms around Ithaca may indicate that temperature plays a greater role in their ecology. None of the study areas was less than 380 m in elevation, and this seems to be about the lower altitudinal limit of *P. m. gracilis* in the vicinity of Ithaca. *P. l. noveboracensis* is much more widespread, being readily obtainable at all elevations and suitable habitats in the area. The general effect of increased altitude is a decrease in temperature. The altitudinal differences involved are not large enough to cause a temperature change of more than a few degrees Centigrade. At elevations above about 360 m the Glaciated Allegheny Plateau around Ithaca is hilly, having been dissected by drainage pattern erosion. This area presents many more shaded, north and east-facing hillsides and greater areas of denser woodlands, than the more level, more extensively farmed area, whose elevations are below this figure. The combination of higher altitude and shaded slopes is apparently the explanation for the occurrence of *P. m. gracilis* in only the hilly areas.

Some work has been done on which to base the use of plants as indicators of physical conditions of a habitat. Oosting & Hess (1956) summarized literature on ecological relations of *Tsuga canadensis* in north-central and northeastern United States. They concluded that this species occupied sites which were intermediate in amount of moisture between drier *Quercus-Carya* sites and moister *Fagus-Acer* sites. In North Carolina they found that, on a bluff, *Tsuga canadensis* occupied an intermediate position between beech at the mesic bottom, and chestnut oak at the more xeric bevel of the bluff, with Piedmont oaks at the top of the bluff. Hills (1952) has indicated that a hemlock-yellow birch association occurs in

habitats of colder-than-normal microclimate over dry soil, and that an oak-chestnut association occurs in habitats with warmer microclimate over dry soil. The positive association between *P. m. gracilis* and T.B.A. (Table 13), and the negative association between *P. m. gracilis* and species typical of the Oak-Chestnut Forest region (Table 13), may indicate that *P. m. gracilis* was attracted to habitats of colder microclimate and avoided those with warmer microclimate. Coefficients of association indicated that the opposite condition generally held for *P. l. noveboracensis* and the same plant species. *P. m. gracilis* was usually positively associated with *Fagus grandifolia* and *Acer nigrum*, while *P. l. noveboracensis* was usually negatively associated with these species (Table 13). These associations were not consistent, and there were some contradictions in the data for Smiley's Woods. This lack of consistency in the measure of interspecific association of *P. m. gracilis* and *P. l. noveboracensis* with these climatic climax species suggests that this woodland type may be the zone of most frequent ecological overlap between the two mice. This seems reasonable in light of the normal microclimate ascribed to this woodland type by Hills (1952).

Although habitats with *Fagus grandifolia* and *Acer nigrum* may have been areas of ecological overlap of these forms of *Peromyscus*, they were apparently not areas of population and home range overlap. The coefficients of association between *P. m. gracilis* and *P. l. noveboracensis* (Table 6) generally indicate negative association between the species. When this association was measured in the presence and absence of *Fagus grandifolia* and *Acer nigrum*, it was found that all but two measurements were not valid because one species was present at less than five stations in the plus or minus sub-sample (L. C. Cole, personal communication). The two valid coefficients of partial association were not statistically significant. There is no indication that *P. l. noveboracensis* and *P. m. gracilis* were more positively associated in habitats with *Fagus grandifolia* or *Acer nigrum*.

POPULATION PRESSURE AND INTERSPECIFIC ANTAGONISM

These two factors may have been operating to determine the local distribution of the two mice. High densities of individuals of one species in a preferred habitat may force some individuals into other habitats. This may modify the local distribution of animals to a marked degree, as was apparently the case with *P. m. gracilis* occurring in sparsely vegetated fields (Barbehenn & New 1957). Countering this tendency to invade other habitats may be a form of interspecific antagonism. Territories and home sites may be more vigorously defended by animals in their preferred habitats. Invaders of a different species, out of their own preferred habitat, may be at a psychological disadvan-

tage in trying to establish territories in this suboptimum habitat.

It is not possible to determine whether these factors were operating to produce the distributions observed in this study. In Smiley's Woods, the occurrence of *P. l. noveboracensis* at the western edge of the trapping grid in both 1955 and 1956 suggests that this species may have had a center of distribution to the west of the trapping grid. This area was occupied by a strip of open woodland about 90 m wide, and beyond that, a cultivated field. This habitat was quite suitable for *P. l. noveboracensis*. The extent to which this animal occupied the western part of the study area may have indicated the level of the population in the region to the west of the study area. The individuals present on the trapping grid may have been forced there by overcrowded conditions in the area to the west of the study area. The association of *P. l. noveboracensis* with *Fagus grandifolia* and *Acer nigrum* may have been the result of population pressure rather than selection of a preferred habitat. That this form has a tolerance for a wide range of habitats is not to be overlooked. However, published reports indicated that there was some measure of avoidance of cool, moist habitats. This factor appears to have been operating in this study, as shown by the negative association between *P. l. noveboracensis* and T.B.A. (Table 13). *Fagus grandifolia*-*Acer nigrum* woodland may have been a suboptimum habitat for *P. l. noveboracensis*, but one not so strongly avoided as the *Tsuga canadensis*-*Betula lutea*-*Acer pennsylvanicum* association.

Fagus grandifolia-*Acer nigrum* woodland may also have been suboptimum habitat for *P. m. gracilis*, although not as strongly so as for *P. l. noveboracensis*. Coefficients of association for *Peromyscus* species and *Fagus grandifolia* indicate a more frequent positive association between *P. m. gracilis* and *Fagus grandifolia* than between *P. l. noveboracensis* and *Fagus grandifolia* (Table 13). Figs. 1 and 4 indicate that *P. m. gracilis* was more abundant in the eastern part of the Smiley's Woods study area where *Tsuga canadensis*, *Betula lutea* and *Acer pennsylvanicum* were dominant. It is possible that the spread of *P. m. gracilis* individuals to the western part of the study area in 1956 was due to population pressure in the eastern portion of the area.

At Connecticut Hill, in 1956, *P. m. gracilis* was abundant over the eastern portion of the study area. (Fig. 5). It was trapped to a small extent where *Quercus Prinus* occurred (upper right corner of Fig. 5). Presence of *P. m. gracilis* in this area may have been due to population pressure.

Population pressure may have been countering selection of preferred habitat by *P. l. noveboracensis* at Arnot Forest in 1956. The density of *P. l. noveboracensis* was high, estimated at 8.23/hectare (3.33/acre) for the entire study area. The area south of the watercourse (which ran from N-12 to D-6) was an *Acer nigrum*-*Fagus grandifolia*-*Tsuga cana-*

densis woodland. Of the 89 stations, *Acer nigrum* was present at 84, *Fagus grandifolia* at 56, and *Tsuga canadensis* at 34. The only oak present was *Quercus borealis*, at two stations. *P. l. noveboracensis* occurred at 48 stations in this area. These occurrences may represent movements into this area, dominated by climax vegetation, because of overcrowding in the area on the north side of the watercourse (Fig. 6).

Although it may have been operating, there was no evidence to indicate that interspecific antagonism was a factor in the distribution of these forms of *Peromyscus*. Harris (1952) concluded from the work of others that *P. m. bairdii* and *P. l. noveboracensis* were not antagonistic toward each other. The observations at Arnot Forest, lines N through T, seem to indicate that no significant antagonism existed between *P. m. gracilis* and *P. l. noveboracensis*, although the -0.27 coefficient of association between these species suggests a slight tendency toward non-association. It is possible that some of the negative association between *Peromyscus* species (Table 6), and the tendency of these animals to occupy different parts of the study area, may have been due to behavior of the individuals. If present, this behavioral factor may have operated to enhance the ecological separation of the species.

CONCLUSIONS

On three selected areas on which studies were conducted, *Peromyscus maniculatus gracilis* and *P. leucopus noveboracensis* generally occupied somewhat different parts of each study area. This is indicated by coefficients of interspecific association (Table 6) and by the trapping data in Figs. 1-6.

P. m. gracilis was generally positively associated with plant species typical of the Hemlock-White Pine-Northern Hardwoods Forest region. It was more positively associated with edaphic (or physiographic) climax species, *Tsuga canadensis* (hemlock), *Betula lutea* (yellow birch) and *Acer pennsylvanicum* (striped maple), than with the climatic climax species, *Fagus grandifolia* (beech) and *Acer nigrum* (sugar maple). *P. m. gracilis* was negatively associated with plant species typical of the Oak-Chestnut Forest region. These species occurred as developmental vegetation or physiographic climax vegetation in the region of the study areas.

P. l. noveboracensis was positively associated with plant species typical of the Oak-Chestnut Forest region. It was usually negatively associated with species typical of the Hemlock-White Pine-Northern Hardwoods Forest region, particularly *Tsuga canadensis*, *Betula lutea* and *Acer pennsylvanicum*. These species have been considered an edaphic climax association of cooler-than-normal habitats.

Reasons for the tendency toward ecological separation of *P. l. noveboracensis* and *P. m. gracilis* were not directly ascertainable. It did not appear that any psychological factor was involved, such as

response to coniferous versus deciduous trees or to amount of ground vegetation. The kinds of woodland occupied by *P. m. gracilis* and by *P. l. noveboracensis* were presumably different in soil moisture and soil temperature. *P. m. gracilis* habitats appeared to be cooler and moister than those occupied by *P. l. noveboracensis*. From experimental work it appeared probable that moisture or humidity would have had no differentiating effect on habitat selection by individuals of the two forms. No comparative experimental information was available for the two species regarding temperature preference during the breeding season. Indirect evidence from altitudinal range differences between the two forms, and from indicator plants in the habitats, suggests that *P. m. gracilis* may select cooler habitats than *P. l. noveboracensis*.

On the study areas, there appeared to be microclimates ranging from warmer-than-normal to cooler-than-normal. These were presumably indicated in this order by vegetation typical of the Oak-Chestnut Forest region, climatic climax vegetation of the Hemlock-White Pine-Northern Hardwoods Forest region, and an edaphic climax vegetation of this forest region. *P. l. noveboracensis* appeared to be most abundant in habitats of warm microclimate, and *P. m. gracilis* in habitats of cool microclimate. Habitats in which *Fagus grandifolia* and *Acer nigrum* were dominant were presumably habitats of normal microclimate (Hills 1952). Inconsistent and neutral coefficients of association between each species of *Peromyscus* and the plant species listed in Table 3 occurred most often with *Fagus grandifolia* and *Acer nigrum*. This woodland association appeared to be the zone of most frequent ecological overlap between the two forms of *Peromyscus*.

Crombie (1947) has reviewed literature on interspecific competition and has called attention to a special case for the application of Gause's "hypothesis." If two competing species meet along an environmental gradient, each end of which favors one species, there would theoretically be a point on the gradient, on either side of which one species would be superior to the other. In a stable environment, this point would mark a definite boundary, since each species would prevail over the other in its preferred habitat. In natural environments, the conditions are always changing, and this boundary would be continually moving and describing an area in which the two species would be in a state of unstable overlap. It seems that *Fagus grandifolia*-*Acer nigrum* woodland on these study areas was such a zone of unstable overlap. One of the constantly changing conditions in these natural environments was the change in population density of each species. Population pressure apparently caused movement of individuals from overcrowded, preferred habitats to other habitats, and increased the extent of ecological overlap.

Lack (1945) has pointed out another factor which

could allow permanent ecological overlap of two species with the same ecology. If both species were kept low in number by predation or parasitism, the food supply would always be adequate, and no competition would occur between species for food. Whether predation or parasitism were such factors in allowing these species to exist together in the same area is not known. Perhaps they do operate effectively in times of high mouse population densities.

No evidence was present in this study that indicated that behavioral factors, such as interspecific antagonism, played a part in determining the local distribution of the forms of *Peromyscus*. The distribution of individuals of each species on some of the study areas suggests that this factor may have been operating.

The main circumstance in the co-existence of *P. l. noveboracensis* and *P. m. gracilis* on the study areas appears to have been selection of somewhat different habitats, perhaps mainly because of differences in microclimate.

SUMMARY

A study was made of the ecological relationships of the deer mice, *Peromyscus leucopus noveboracensis* and *P. maniculatus gracilis*, where both were present on three woodland areas near Ithaca, in central New York. Trapping grids with an interval of about 14 m (45 ft) were laid out on the study areas. Mark-and-recapture studies were conducted during the summers of 1955 and 1956. Snap-trapping was done in the summer of 1957. The vegetation of each area was analyzed by the use of sample plots at trap stations. L. C. Cole's method of calculating a coefficient of interspecific association was used to measure the association between each species of mouse and various species of conspicuous plants. Behavior of captive mice was observed to determine whether interspecific antagonism was present. Water consumption of individuals of the two species was measured to determine whether interspecific differences existed. Petersen population estimates were made of each species for each trapping period, and population densities were calculated for each study area.

Results indicated that there was some ecological separation of the two species. *P. l. noveboracensis* was positively associated with plant species typical of climax vegetation of the Oak-Chestnut Forest region. These were *Quercus prinus*, *Q. borealis*, *Q. alba*, *Rhododendron nudiflorum*, *Vaccinium angustifolium*, *Gaultheria procumbens* and *Pteridium aquilinum*. These species are part of developmental stages of vegetation of the Hemlock-White Pine-Northern Hardwoods Forest region, in which the study areas were located. *P. m. gracilis* was negatively associated with these species of the developmental vegetation. It was usually positively associated with plant species typical of the Hemlock-

White Pine-Northern Hardwoods Forest region. These were *Tsuga canadensis*, *Betula lutea*, *Acer pennsylvanicum*, *Polystichum acrostichoides*, *Dryopteris noveboracensis*, *D. spinulosa*, *D. marginalis*, *Fagus grandifolia* and *Acer nigrum*. *P. m. gracilis* was most positively associated with an edaphic climax association which is said to occur in habitats of dry soil and a cooler-than-normal microclimate. Species in this association were *Tsuga canadensis*, *Betula lutea* and *Acer pennsylvanicum*. *P. l. noveboracensis* avoided these species and others characteristic of the Hemlock-White Pine-Northern Hardwoods region. However, it was at times positively associated with the climatic climax species, *Fagus grandifolia* and *Acer nigrum*. Conversely, *P. m. gracilis* was at times negatively associated with these plant species. These contradictory (plus additional neutral) coefficients of association between each species of *Peromyscus* and the climatic climax plant species appeared to indicate that *Fagus grandifolia*-*Acer nigrum* woodlands were places of ecological overlap between the species of *Peromyscus*. Population pressure within these species may have increased the amount of overlap.

Reasons for the ecological separation of the species were not brought out in the study. Information from various sources indicates that it is improbable that differential habitat selection occurred on the basis of soil moisture, humidity near the ground, amount of ground vegetation or presence of coniferous versus deciduous trees. Studies conducted in this area have shown that, during the summer months, surface soil temperatures in sugar maple-beech-yellow birch woodland were 3.3-3.9°C (6-7°F.) lower than in chestnut-oak woodland. Surface soil temperatures may have been a significant factor in differential habitat selection by *P. l. noveboracensis* and *P. m. gracilis*.

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ERRATA

Two errors were introduced into the paper on "Vegetation of the Siskiyou Mountains, Oregon and California" by R. H. Whittaker by incorrect entry of galley proof corrections:

1) Pages 289-290. The paragraph beginning "These results..." on page 290 should follow the first paragraph on page 289 ending "...on serpentine—34.9, 32.2, 34.7" and precede the section on "Transsect Tables."

2) Page 321. The equation in the second paragraph should read, $\beta = \frac{\gamma}{\alpha}$

A note from the author on uncertain taxonomic status of the population designated *Arctostaphylos cinerea* on gabbro was not received in time for inclusion.



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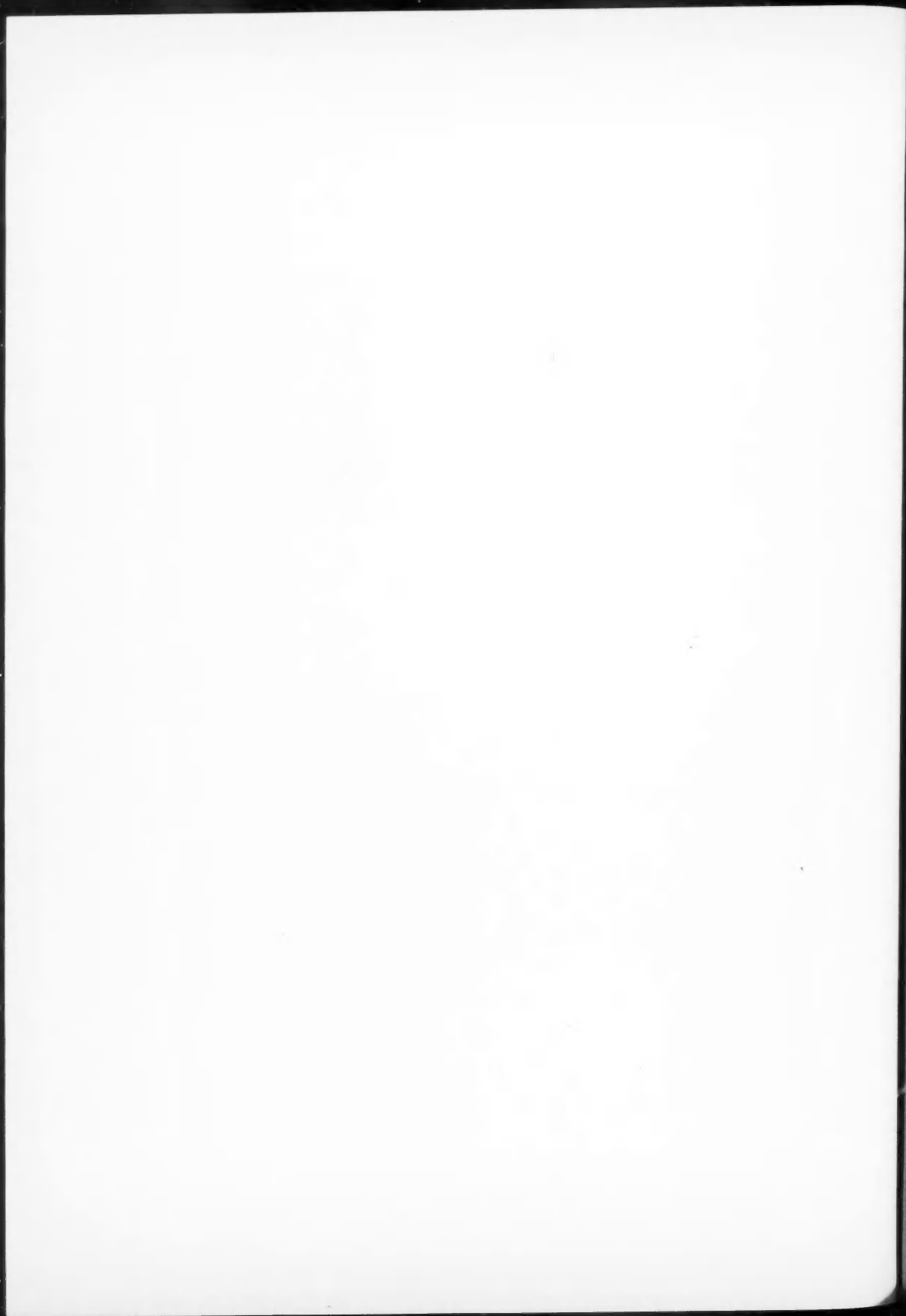
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